PATTERNS AND RATE OF WOODY VEGETATION CLUSTER DEVELOPMENT IN A SEMI-ARID SAVANNA, NATAL, SOUTH AFRICA

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Dedication

Hierdie werk is opgedra aan my ouers. Behalwe vir totaal onselfbaatsugtige aanmoediging en finansiële steun, is ek my groot voorliefde vir die natuur en kennis aan hulle verskuldig.

Preface

This research was undertaken whilst in the employ of the Natal Parks Board as Nature Conservation Scientist for Southern Natal and later on for South Zululand. I thank my employers for the opportunity to undertake this work and for logistic and material support during the study. They also provided me with a study bursary for which I am very grateful and access to the Weenen Nature Reserve. I wish to thank especially Mr Peter le Roux for his support in the motivation for this project, and all the staff at the Hluhluwe Research Centre who had to put up with my grumpiness during the writing-up phase.

I am greatly indebted to my academic supervisors, Prof Dick Yeaton and Dr Ed Granger for their support, motivation and constant readiness to advise or discuss problems without which I would never have been able to do this work. I especially thank them for all the trouble they must have undergone to correct my version of English.

I thank Professor J. van Staden and all the staff of the Botany Department at the University of Natal, Pietermaritzburg for providing facilities for two months at the Department during the write-up phase and for arranging a University of Natal Postgraduate Bursary during the first year of registration. I thank the University of Natal's Research Fund for a grant to Professor R.I. Yeaton which underwrote the costs of the aerial photographs. Also, I thank Dr. M. Aiken and Mr F. Smith, who assisted me extensively with the workings of the different software packages that I employed in the analyses of the data. Messrs D. van Zyl and D. Furniss helped me collect the data and provided companionship at some very lonely camp sites. I am grateful to both of them. Finally, Mr P. Opperman of 'Darkest Africa' and Mr P. Gill of 'Ellenaberg' kindly allowed me to conduct much of this study on their farms. I thank them for thought-provoking discussions and valuable background information on the histories of their farms and of the Weenen District.

Declaration

All field work described in this dissertation was carried out in the Weenen District, Natal from March, 1991 to April, 1992 under the supervision of Prof. R.I. Yeaton and Dr. J.E. Granger.

This study represents original work by the author, and has not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

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Postscript

Zak le Roux died tragically on his birthday 5 March 1993 whilst canoeing on the Msinyathi River. We, his supervisors, were able to locate the penultamate draft of his thesis and took it upon ourselves to rectify only the superficial problems which we found. Thus, the ideas, data, interpretations and discussions and conclusions remain Zak's. It is our conviction that, given the stage to which he had taken this work and the contribution which we believe that it makes to our understanding of the Natal bushveld, this thesis merited posthumous submission for the degree for which it was registered.

J.E. Granger

p.p. R I YEATON away on leave
Supervisor

Date : 23 July 1996.

J.E. Granger

J E GRANGER
Co-supervisor

Date : 23 July 1996.

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CHAPTER ONE: INTRODUCTION

1.1 The `Natal Bushveld'

The term `savanna' has been used in so many ways that it has become impossible to use it in an unambiguous sense (White 1983). However, it remains a convenient term to describe the desert-savanna-forest continuum (Hadley 1985, Menaut *et al* 1985). Savanna generally describes tropical and subtropical formations where the grass stratum is continuous and important, although occasionally interrupted by trees and shrubs, where bush fires occur from time to time, and where the main growth patterns are closely associated with alternating wet and dry seasons (Bourliere & Hadley 1970, 1983).

Savanna occurs across a mean annual rainfall gradient from 300 mm to 1000 mm. Mean annual rainfall of 600 mm is used to distinguish between climatically determined semi-arid and humid savanna. Arid or semi-arid savanna is characterised by, at least, seasonally limited available moisture and not necessarily by low soil nutrient status. Nutrient-poor savanna can occur with a mean annual rainfall of approximately 1500mm (Walker 1985).

Savanna in southern Africa is primarily arid. It is characterised by the co-dominance of fire-adapted hemicryptophytes and phanerophytes. This formation is approximately 959 000 km^2 in extent and covers approximately 46% of southern Africa. It is the dominant vegetation type of most river basins, particular along the eastern flanks of southern Africa. In southern Africa, savanna extends from north of 22°S into central Namibia, Botswana, higher rainfall areas of the northern Cape, the northern two-thirds of the Transvaal, lower altitudes of the northwestern Orange Free-state, Mozambique, central and east Swaziland, lower altitudinal areas of KwaZulu/Natal (formerly Natal), Transkei and the eastern Cape Province, and some valleys in the southern Cape. Most of the lower elevational areas in KwaZulu-Natal are classified as part of this savanna (Rutherford & Westfall 1986). However, following Edwards's (1983) definition that the term describes a vegetation type with a herbaceous, mainly graminoid layer with an open upper layer of woody plants, almost all of KwaZulu-Natal can be classified as savanna.

In South Africa, savanna associations characterised by a conspicuous tree component are commonly called `bushveld'. The term `Natal bushveld' refers to arid and semi-arid savanna, characterised by a conspicuous tree component. Natal bushveld comprises portions of Acocks (1953) Northern Variation of the Valley Bushveld (Veld Type 23a), the Lowveld and the Arid Lowveld (Veld Types 6 and 10). The Northern and Southern Tall Grassveld types (Veld Types 64 and 65) resemble a transition from bushveld to grassland and are often referred to as bushveld or thornveld.

KwaZulu-Natal is situated on the east coast of southern Africa. Although a small province relative to the other provinces of the Republic of South Africa, KwaZulu-Natal's physiography varies enormously over short distances. From the coast to the summits of the Drakensberg, relief exceeds 3 385 m (King 1982). This steep gradient, due largely to monoclinal flexing that has taken place parallel to the coast, is incised by many deep valleys which traverse the whole width of KwaZulu-Natal resulting in a very broken topography (King 1982). For example, the valley of the Tugela River is 900 m deep in places. Apart from sediments along the coastal margin, the geological formations of KwaZulu-Natal were in place before the breakup of Gondwanaland *c.* 100 million years ago (Du Toit 1954, King 1982). The river valleys expose several geological formations. The most common of these formations found in the deep valleys is the Ecca series of the Karroo system (Du Toit 1954, King 1982). The Ecca series comprises shales, mudstones and some sandstones of the early Mesozoic era. Towards the coast most valleys incise into the Natal Group Sandstone formation and Basement granites, gneisses and quartsites (King 1982, Partridge & Maud 1987).

Natal bushveld is the predominant vegetation type in these valleys extending from sea level up to an altitude of *c.* 1500 m (Phillips 1973). At higher altitudes, bushveld is usually associated with localised arid conditions induced by topography and by the intensive, longterm utilisation of grasslands (Edwards 1967). At altitudes below *c.* 600 m bushveld shows many affinities with the vegetation of the coastal areas (Acocks 1988).

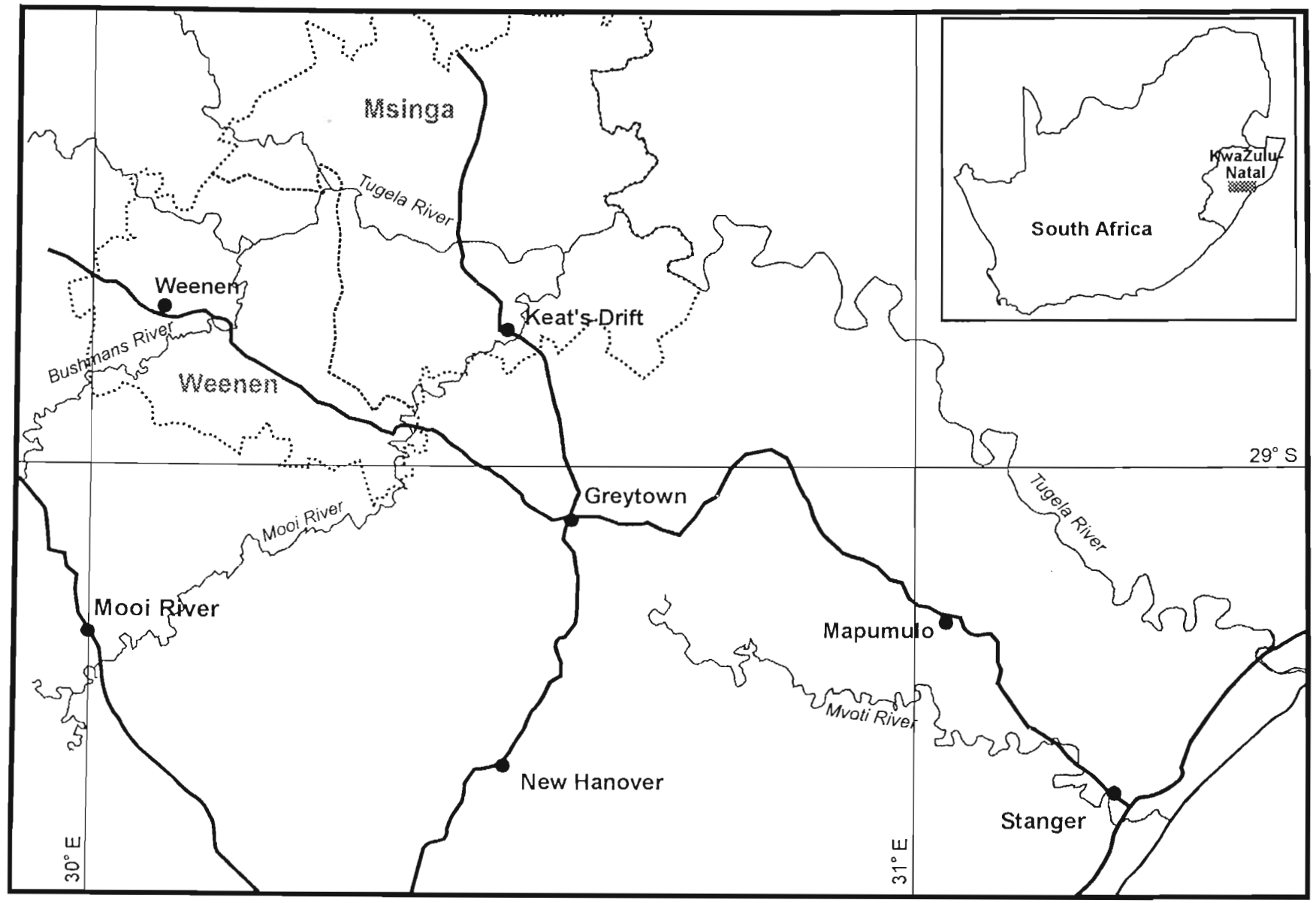

Figure 1.1 Location of Study Area in KwaZulu-Natal, South Africa

The location of the study area is indicated in Figure 1.1.

Rain occurs mainly in summer (Figure 1.2) and is very erratic (Figure 1.3). For example, the longterm mean annual rainfall for three stations in the central Tugela Valley (Mfongosi, Muden, Weenen) is 620 mm, but varies from 260 mm to 1400 mm (Edwards 1967).

Bushveld areas in KwaZulu-Natal generally experience extreme temperatures. For example, the longterm mean daily maxima for Mfongosi, Muden and Weenen the general region of the study, were just over 30°C for the three hottest months December, January and February, and over 25°C from September to April for the period 1951 to 1955 (Edwards 1967). Absolute daily maximum temperatures during this period varied from 40°C to 45 C. Mean daily minima were 6.7 C, with an absolute minimum, 0.8°C recorded at Mfongosi. Severe frost occurs at many places in bushveld areas of KwaZulu-Natal from May to July (Edwards 1967).

Natal bushveld has a long history of human habitation and intensive exploitation (Bryant 1929, Feeley 1987, Maggs 1989, Mazel 1989). This exploitation has had an important influence on the development of the vegetation (Feeley 1978, 1987; Granger & Prins 1991). The combination of erratic and low rainfall, high temperatures, steep slopes and prolonged intense exploitation by humans has helped to promote the arid and semi-arid, often sparsely vegetated conditions characteristic of these valley systems. It has therefore been suggested that increased global warming (Ellery *et al* 1991, Emanuel *et al* 1985a,b) and the current intensive exploitation by subsistence farmers, especially in rural KwaZulu-Natal will exacerbate these arid and semi-arid conditions resulting in the expansion of bushveld rangelands.

1.2 Bushveld vegetation development, succession and `bush encroachment'.

Most studies of Natal bushveld have been of a descriptive and anecdotal nature (Bews 1912, Henkel 1937, Adamson 1938, Bayer 1938, West 1951, Wells 1959, Edwards 1967, Moll 1976, Acocks 1988). Various bushveld types were identified and described by these authors and vary from open grassland to *Acacia*-dominated

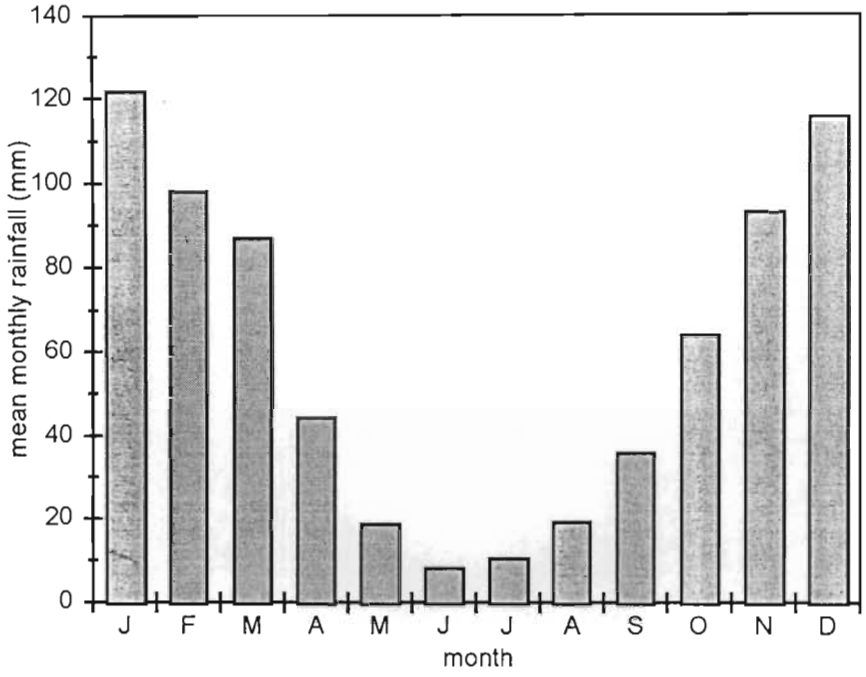

Figure 1.1. Mean Monthly rainfall (mm) from 1926 to 1983 (Weenen District).

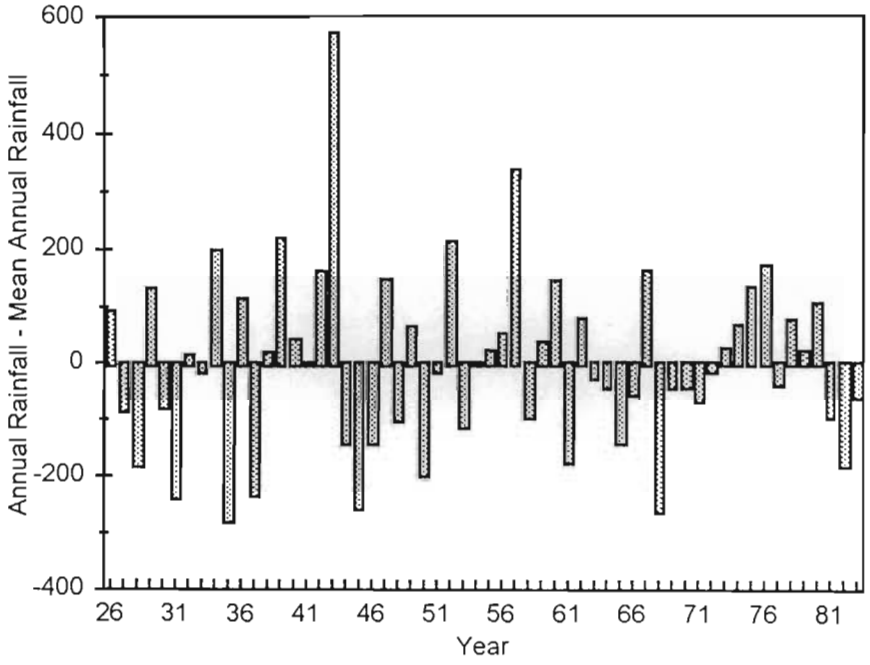

Figure 1.3. Variation of annual rainfall (mm) from the long-term mean (710 mm) from 1926 to 1983 (Weenen District).

savannas to semi-deciduous or succulent woodland, shrubland and forest. In addition, various temporal replacement sequences of different community types have been described or postulated with very little long-term monitoring to corroborate them.

Bews (1917) described the invasion of grasslands by *Acacia* species followed by the establishment of broadleaved shrubs at Bisley Valley near Pietermaritzburg. In so doing he classified the woody species into broad functional (successional) groups. Bews (1917) proposed that grasslands were first invaded by *Acacia nilotica* **(L) Willd.ex Delile** which then facilitated the establishment of later successional species. Later West (1951) suggested that much of the bushveld in the Weenen District and especially in the higher altitude areas near Estcourt was the outcome of recent invasion of *Acacia* species into grasslands. Comins (1953), in his account of the plant ecology of the Albert Falls area of the KwaZulu-Natal Midlands, described the invasion of grassland by `heliophylous' *Acacia* species followed by more `hygrophylous' plants which soon overtop the early invaders to form a bush clump community. He also reported that grasslands that had been ploughed were generally more prone to invasion by woody plants. Killick (1959) observed that degraded grasslands at Table Mountain in the Mgeni Valley were being invaded by *Acacia* species and that different types of woodland then developed depending on soil type and local humidity of the site. He also suggested that heavily exploited woodlands would be replaced by succulent thicket. Edwards (1967) found that grassland at higher (above *c.* 600m) elevations in the Tugela basin was being replaced by *Acacia* woodlands while at lower (below *c.* 600m) altitudes, microphyllous and semi-deciduous woodlands were being replaced by succulent scrub. Wells (1959) suggested a similar pattern for vegetation in the Nagel Dam area of the Mgeni Valley. In a quantitative description of the plant ecology of Ntshongweni in the lower Mlazi Valley, Morris (1967) showed how an abandoned Iron-Age farming site, locally known as a `kraal', changed from an old-field to grassland, to *Acacia* woodland, and finally to a semi-deciduous broadleaved and succulent community in 40 years. By 1990 (*c.* 25 years after Morris described this site) the vegetation had changed to a succulent thicket dominated by *Euphorbia tirucalli* **L.** and *E.ingens* **E. Meyer ex Boiss** (personal observation). In a larger scale study of the vegetation of the Three Rivers Region (Mgeni, Mlovu and Mlazi Valleys), Moll (1976) found that *Acacia* woodlands are the

most common vegetation type and that they are expanding their range due to the invasion of grasslands by *Acacia* species.

Thus, the general trend of vegetation change in seasonally arid areas of KwaZulu-Natal seems to be a large scale conversion of grassland to savanna and an increase in the density and stature of woody plants in bushveld areas. Recent encroachment of semi-desert and shrubland species into grassland and open savanna woodlands is not unique to KwaZulu-Natal. Such encroachment has been described in most semi-arid savanna and grassland regions of Africa (Barnes 1979), Australia (Harrington *et al* 1984), South America (Buchner 1987), and North America (Buffington & Herbel 1965, Blackburn & Tueller 1970, Herbel *et al* 1972, Hobbs & Mooney 1986, Archer *et al* 1988). In South Africa this phenomenon is popularly called `bush encroachment' (Trollope *et al* 1990). Although the phenomenon has been widely observed, the rates, patterns and dynamics of the process have seldom been quantified (Archer *et al* 1988). Generally bush encroachment leads to a reduction in production and stature of the herbaceous layer. In addition, the structure of bush-encroached savanna reduces the visibility of game and domestic stock. Traditional objectives of rangeland utilisation often need to be compromised when bush encroachment occurs. Expensive and often unsuccessful bush clearing operations are necessary. This option drastically reduces the profit margin of most traditional land-uses such as agricultural practices based on cattle, sheep or tourism. As a result bush encroachment often has negative connotations.

Vegetation community development towards a climatic climax (Clements 1916) has for decades been the cornerstone of South African rangeland science (Smuts 1926, Killick 1959, Acocks 1953 & 1988). This concept has been expanded to acknowledge the effects of perturbations such as herbivory and fire in deflecting the climax to `stable equilibrium states' or `secondary climaxes' (Gleason 1926, Tansley 1935, Phillips 1935, Weaver & Clements 1938, Dyksterhuis 1949, Acocks 1953 & 1988).

Classical rangeland management practices are based on maintaining productive `stable equilibrium states' of vegetation. Rangelands were first classified by type (climatic climax) and then on condition (successional status). `Veld' or range condition was then compared to chosen 'benchmark sites' along a gradient of

herbivory intensity. A `benchmark site' is subjectively chosen and usually represents a vegetation condition that is judged best suitable for the prescribed range management objectives. Herbaceous species composition, basal cover of the herbaceous layer and the degree of bush encroachment are usually used as criteria when identifying benchmark sites (Foran 1976, Tainton 1981). This model of vegetation response to various levels of utilisation might be relevant to some rangelands, but it fails to explain the full range of spatial and temporal variation that can be observed in arid and semi-arid rangelands (Gleason 1926, Drury & Nisbet 1973, Connell & Slatyer 1977, Westoby 1979). This approach also fails to address various rangeland management objectives (*e.g.* the conservation of species diversity, the management of a heterogeneous vegetation mosaic, the maintenance of ecosystem resilience) (Goodman 1991, Mentis *et al* 1989).

Traditionally, the dynamics of savanna rangelands have been explained within the framework of primary and secondary determinants (Teague & Smit 1992). Primary determinants are mainly rainfall and soil nutrient status (Walker 1985). Variation within the pattern determined by the primary factors is ascribed to the combined impact of secondary factors such as fire (Frost 1985, Sweet & Tacheba 1985, Sabiiti & Wein 1988, Dublin *et al* 1990), herbivory (Skarpe 1990a,b; Belsky 1984; Reuss & Halter 1990) and human activities (Kelly & Walker 1976, Ellis & Swift 1988, Blackmore *et al* 1990). Permanent or semi-permanent changes, which occur in savanna communities, are invariably associated with changes in abiotic variables which are maintained through the activities of the biota. Bush encroachment and desertification are generally blamed on the collapse of the `equilibrium' or `balance' in `fragile' ecosystems (May 1977) caused by human exploitation (Roberts 1985), changes in global climate (Emanuel *et al* 1985a,b) and changes in the composition of the faunal component of landscapes (Janzen 1986). One obvious group of properties, about which virtually nothing is known in savannas, concerns the ways in which the plant species interact (Walker 1985). As a result, complex causal factors of succession in savanna rangelands are difficult to understand.

The distribution and abundance of plants is not dependent directly on physical-chemical habitat conditions (Van Hulst 1980). Recent work in South African savanna supports this contention. A gradient study in the Sabi-Sand area of the eastern

Transvaal showed there to be a lack of evidence to conclude that plant species distributions are determined by soil moisture and soil nutrient distribution (Ben-Shahar 1990). Rather, bush encroachment is a complicated process likely to be driven by species responses to disturbance events. Nott (1991) showed that in the Hluhluwe-Umfolosi Game Reserve Complex of KwaZulu-Natal there exist only weak correlations between plant species distributions, management history, altitude, rainfall, and soil type. He suggested that facilitation and competition among component species are important determinants of plant species distributions and that they mask the influence of abiotic variables. In the Albert Falls area of KwaZulu-Natal a fenceline contrast up a slope between a game reserve and a cattle ranch shows significant differences in the plant communities (Le Roux & Yeaton 1992). The woody vegetation on the cattle ranch is more species rich with eleven woody species being recorded. In contrast, only five woody species were recorded in the game reserve. Mature *A. nilotica* trees, the seed of which is dispersed by large herbivores, as well as seedlings of broadleaved trees were distributed evenly over the slope in the cattle farm. In the game reserve mature *A. nilotica* and seedlings of broadleaved trees occurred only at the top of the slope and near an old 'kraal' site. Thus, the land-use history of a site has a greater effect on plant species distributions than their position along the complex environmental gradient found over the slope.

In many situations there often exist only weak correlations between abiotic factors and plant species distributions. Biotic interactions, such as facilitation and competition are probably more important determinants of plant species distribution and vegetation development. One result of these biotic interactions is that different `stable equilibria' or savanna community types represent different successional stages distributed across the landscape in response to disturbance.

In arid and semi-arid areas the development of vegetation structure seems to be determined by stochastic disturbance that retards linear succession resulting in complex combinations of cyclical successions (Yeaton 1978, 1988; Yeaton & Manzanares 1986). The direction of succession seems to be regulated by the life histories and demographic responses of individual species populations to disturbance (Connell & Slatyer 1977, Westoby 1979, Noble & Slatyer 1980).

Invasion of grasslands by trees has been attributed to the differential depth of active roots between the herbaceous and tree layers with trees being able to exploit moisture deeper in the soil and herbaceous plants exploiting moisture at shallower soil depths (Walter 1971, Walker & Noy-Meir 1982, Knoop & Walker 1985). Because grasses have actively growing basal buds, they usually respond more favourably to fire than woody plants with terminal buds. Thus, the occurrence of regular fires can give grasses a competitive advantage over trees where the herbaceous layer is mainly graminoid (Trollope 1982). However, if the soil moisture is below the active depth of the roots of the herbaceous layer, or if fire is excluded through removal of herbaceous biomass (*i.e.* fuel load), trees then have the competitive advantage. Once established, trees can suppress herbaceous growth by reducing light under their canopies. They can also change the species composition of the herbaceous layer (Yeaton *et al* 1989, Nott 1991).

From a number of studies it is evident that woody microphyllous legumes (trees of the family *Mimosoidae)* are the first plants to invade semi-arid grasslands (Bews 1917; Archer *et al* 1988; Brown & Archer 1989; Archer 1989, 1990; Briers & La Cock 1991; Ben-Shahar 1991). These trees then facilitate the establishment of broad-leaved woody plants and succulents (Yeaton & Manzanares 1986; Archer *et al* 1988; Archer 1989, 1990; Valiente-Banuet & Ezcurra 1991).

Failure to develop models of rangeland succession that successfully predict and explain vegetation responses to management actions has produced much conflict concerning the usefulness of succession theory in range management and is a serious downfall of modern rangeland science (Mentis 1989, Westoby *et al* 1989). As yet there is no single model of woody plant succession for the Natal bushveld that is robust enough to explain the development of the vegetation component of different landscapes.

Direct studies of succession in plant communities are difficult because of the time scales and the complexity of species interactions involved. Photographic time series (Archer *et al* 1988), longterm monitoring experiments (Peet & Christensen 1979), carbon isotope ratios in soil (Archer 1990) and data from archaeological sites (Feeley 1987, Granger & Prins 1991) can be used to create time gradients and furnish data on successional trends. Studies of temporal change are often holistic

by nature and they usually accentuate the superorganism characteristics of natural systems. Although such direct studies describe change, they rarely provide much insight to the mechanisms of vegetation dynamics.

Meaningful interpretation of successional trends necessitates a reductionistic approach (Glenn-Lewin 1980, Peet & Christensen 1979). Inferential models based on species attributes (Noble & Slatyer 1980), size/age class structure of component populations (Montana *et al* 1992, Ben-Shahar 1991) and vegetation differences on disturbance gradients (Tueller & Platou 1991) can be used to explain and predict successional trends. Such models are often expressed in terms of Markovian matrix models (Horn 1971, 1974, 1975, 1976). Because the assumptions of these models are rarely met in reality (Van Hulst 1980), it is necessary to broaden the scope of these models to ecosystem level and not concentrate on vegetation dynamics only. Space-for-time models of plant succession (Archer *et al* 1988, Archer 1990) combine inferential models with trends observed from direct methods and can be expanded to incorporate other ecosystem functions (Brown & Archer 1987, 1989). Such models provide insights on the rate and pattern of plant succession and the development of hypotheses of the mechanisms of change. These hypotheses can then be tested through experimentation.

A distinctive two-phase pattern can be recognised in the mesquite woodlands of Texas (Whittaker *et al* 1979a, Archer *et al* 1988). These phases consist of an open continuous phase (herbaceous matrix) and a discontinuous phase (discrete shrub clusters). A similar pattern occurs in semi-arid vegetation in Australia (Whittaker *et al* 1979b) and Chile (Fuentes *et al* 1984, 1986). Field observations in KwaZulu-Natal (Bews 1917, Comins 1953, Edwards 1967) and Texas (Archer *et al* 1988) suggest that the shrub clusters of the two-phase landscape are organised around an early pioneer plant (invariably a microphyllous legume) and that monophasic woodlands are possibly formed from the coalescence of these shrub clusters. It can therefore be inferred that the life history of individual shrub clusters will resemble the development of bushveld vegetation.

Synthesis of descriptive studies of the KwaZulu/Natal bushveld reveals that the vegetation structure of this bushveld can be described as comprising four distinct phases which occur in a mosaic across the landscape (Bews 1917, Comins 1953,

Edwards 1967). These phases are (i) an open grassland phase, (ii) an open savanna phase where single trees occur randomly throughout a grassland matrix, (iii) a bush cluster phase where discrete bush clusters occur in a matrix of grassland or open savanna, and (iv) a closed-canopy woodland.

Because of the apparent similarities between vegetation structure and function in KwaZulu-Natal and Texas, it was decided to use the approach of Archer *et al* (1988) to describe the pattern and rate of succession in the local bushveld. This approach allows one to make use of Clementsian succession theory as distinct steps in the life history strategies of individual species populations (MacMahon 1981). Such usage avoids the holistic concepts of a directed pathway to a single climax stage and of the community as a superorganism. Quantitative description of the species and size-class composition of vegetation clusters and a photographic time series are used to describe the pattern of vegetation cluster growth. The `life histories' of vegetation clusters are then modelled to create a successional gradient (*i.e.* set of progressive successional stages) against which the response of different species populations can be ascribed.

1.3 Objectives

The primary objective of this research is to produce a model of plant succession for the Natal bushveld and a functional classification of the woody species that occur in the Weenen District of the Tugela Basin in particular. This can be useful to (i) generate hypotheses of plant interactions for future experimentation and (ii) to manage savanna rangeland resources in KwaZulu-Natal.

Specific goals of this study were to:

(1) Describe the rate of vegetation cluster growth in the Weenen District over the period 1940 to 1985 for which aerial photography is available.

(2) Describe the pattern of vegetation cluster growth using quantitative descriptions of the species and size-class composition of vegetation clusters.

(3) Determine the influence of selected land management practices on vegetation development.

(4) Classify woody plant species functionally into successional guilds.

(5) Compare these functional attributes with those of semi-arid savannas in other parts of the world.

1.4. Study area

The study was conducted in the Weenen Magisterial District of KwaZulu-Natal, South Africa. The Weenen District is situated in the northern midlands of KwaZulu-Natal in the lower reaches of the Bushmans River Valley where it forms part of the large interior basin of the Tugela Valley (Figure 1.1). The long-term (1926 to 1983) mean annual rainfall is 660 mm, but this varies from 400 mm to 1119 mm (Weather Bureau 1965). The geology comprises mainly shales and sandstones of the Ecca formation of the Karroo System (Kent 1980). Dolorite outcrops form the intervening ridges, while Ecca shales are the most frequently encountered rocks in the valleys.

West (1951) classified the vegetation of the Weenen District into : dense succulent scrub of the valleys; *Themeda*-grassland in the process of transition to thornveld, and open *Themeda-Hyparrhenia-Acacia* savanna. At a much broarder scale Acocks (1953) classified the vegetation of this region as being part of Veld Type 23a, the Northern Variation of the Valley Bushveld. In this classification Valley Bushveld is defined as being `dense woodlands with an affinity to the vegetation of the Karoo'. Edwards (1967), in his broad-scale description of the Tugela Basin, classified most of the district as the Semi-deciduous Bush (*Acacia-Boscia-Olea-Schotia* scrub) of the Valley Landscape. The area falls within Phillips's (1973) Bioclimatic Region 10, Interior Lowland.

The Weenen District has a long history of human occupation and intense exploitation. Approximately 7000 years ago the greater part of the Tugela Basin was populated by Stone-Age hunter-gatherers who did not cultivate the land (Mazel 1989). Before then, it was apparently virtually unoccupied. Early Iron-Age (EIA), Bantu-speaking people established themselves in the Tugela Valley around 2000-1500 years ago. By 300 AD EIA people lived there in large villages of up to eight hectares in extent. They cultivated crops and kept domestic stock with sheep, goats

and, to a lesser extent, cattle having been identified among the remains found in archaeological sites. Crops identified from seeds found in these sites include several grains such as bullrush or pearl millet (*Pennisetum typhoides* (Burm.), finger millet (*Eleusine coracana* (**L.**) **Gaertn.** subsp. *africana*) and sorghum *(Sorghum bicolor* (**L.**) **Moench** subsp. *arundinaceum*) and the African melon (*Citrullus lanatus* (Thunb.) Matsumura & Nakai). In areas where iron ore was present villages often had iron smelters. Together with the fact that timber was also used to construct homesteads and stock enclosures, it is inevitable that these EIA villages must have had considerable effects on the surrounding vegetation over the almost 500 years of EIA occupation. For example, a considerable amount of wood, in the order of a few tons per annum, would have been needed for building, domestic use and iron smelting (Maggs 1980). The paucity of sites dating from the period between 800 to 900 AD suggest that adjoining rangelands had been degraded to such an extent that only a much smaller human population could be supported than occurred in previous times. Sites from this period have also yielded a considerably larger number and variety of wild animal bones as opposed to those of domestic animals, suggesting that during the EIA fewer domestic animals were maintained than occurred during the Later Iron Age (LIA) and that the people supplemented their vegetable diet primarily through hunting (Maggs 1989).

The period following *c.* AD 1000 until *c.* 1900 is known as the Later Iron Age (LIA). During this period cattle seem to have assumed far greater prominence in the Iron-Age economy and culture. At the beginning of the LIA people started to live extensively in the uplands beyond the river valleys in areas vegetated by open grassland areas. Most villages were also much smaller than those of the EIA and were often located in apparently defensive positions (Maggs 1989). This suggests that `cattle wars' or rangeland disputes might have been common.

Notwithstanding occupation of the grasslands by LIA agro-pastoralists, those Bantu-speaking people, who continued to occupy the river valleys in particular, carried on exploiting the woody vegetation as a source of material for constructing homesteads and enclosures for stock and as a source of fuel for domestic fires and for iron smelting. Hence anthropogenic alteration of the wooded valleys continued throughout the LIA. West (1951) reported that almost all the land in the Weenen

District, even on very steep slopes, was tilled at some stage in the past. In addition, the archeological remains of numerous LIA sites support contentions by Bryant (1929) that these valleys were densely populated for at least the last few centuries.

Reports of cannibalism in the Jobskop area of the Tugela Basin in the late 18th Century (Bryant 1929) and the severe wars that broke out in the early 19th Century can be explained as the products of large-scale famine due to longterm overexploitation and the resulting deterioration of these rangelands (Guy 1980). During the reign of the Zulu monarchs Shaka (1818-1828) and Dingane (1828-1841), the Tugela Basin was almost completely depopulated as a result of war and famine (Wright & Hamilton 1989). This period of South African history, known as the *Defecane*, was characterised by mass migrations of people from KwaZulu-Natal with the subsequent displacement or even total annihilation of tribes or clans who occupied the interior of southern Africa at this time.

European immigrants, the Voortrekkers, moving from the Cape Colony arrived in the Tugela Basin during 1838 (Ballard 1989). By then it is assumed the vegetation must have recovered to some extent as a result of reduced human population density because the Voortrekkers, who were stock farmers, chose to settle there.

Unlike what occurred in the Americas, the diverse large mammal fauna of southern Africa did not become extinct at the end of the Pleistocene. Rather it can be argued that during the last *c.* 2000 years of settlement by pasturalists, game numbers became reduced due to hunting and competition with livestock. It is well known that since the 15th Century the hunting of elephants for ivory played an increasing role in the regional economy (Wright & Hamilton 1989, Guy 1980). If the LIA made a noticeable impact on wild life in KwaZulu-Natal, then it was certainly during the period immediately following the *Defecane* that game numbers would have increased considerably in most parts of KwaZulu-Natal (Isaacs 1936, MacKeurtan 1930, Fynn 1950, Delegorgue 1990). However, by the end of the 19th Century almost all larger game species had become locally extinct in the Weenen District (Smithers 1986). Apart from limited alluvial plains where irrigation is possible, the largest portion of the Weenen District is suitable only for extensive ranching with cattle and game (Pentz 1949). The establishment of small farms, less than *c.* 1000 ha in extent, led to intensification of stocking rates and cultivation of marginal land

which resulted in severe degradation of rangeland and the collapse of formal agriculture as early as 1865 (West 1951). After this degradation plus increased incidences of stock diseases and theft caused the European agricultural sector to regard most of the Weenen District as an inferior agricultural region. The resulting low land prices and lack of farm development led to the large-scale abuse of the rangelands. By the early 20th Century degradation of rangelands in the Weenen District had advanced to an alarming extent (Scott *et al* 1940).

Since the turn of the century the area has been used either as winter range by cattle farmers, who owned summer grazing farms located at higher elevations, or as labour-tenant farms. The latter were farms on which labourers and their families lived and kept their domestic stock as compensation for seasonal work on the sugarcane plantations of coastal KwaZulu-Natal or on maize farms below the escarpment. Under the labour-tenant system, the greater the number of tenants on the farm, the greater was the profit of the land owner (Lambert 1985). This system led to a concentration of vast numbers of people, cattle, goats and donkeys on these farms and consequently a severe degradation of the vegetation cover and accelerated soil erosion (Edwards 1967). In 1938 it was estimated that 19% of the area was already eroded down to bedrock, while a further 46% was badly eroded and overgrazed (Pentz 1938). Hence much of the Weenen District is almost semi-desert today (Camp 1986).

Sites investigated for this study were located on two farms and a nature reserve in the Weenen District and are referred to by the names of the farms or nature reserve on which they occurred namely, `Darkest Africa' (DA), Mhlumba (MHL) and Weenen (WE) (Figure 1.4). Each property has had a different landuse history, and is currently subjected to a different form of landuse. Past and current landuses may be categorised as follows; (i) little degradation (DA), (ii) severe degradation followed by intensive rehabilitation (WE) and (iii) severe degradation without intensive rehabilitation (MHL). Additional data were collected at sites located near Keats Drift in the Msinga District (MS) which is currently densely inhabited by subsistence farmers and in the Tugela Valley below Maphumulo (MAP) where large bush clusters, which may be representative of late successional bushveld, occur .

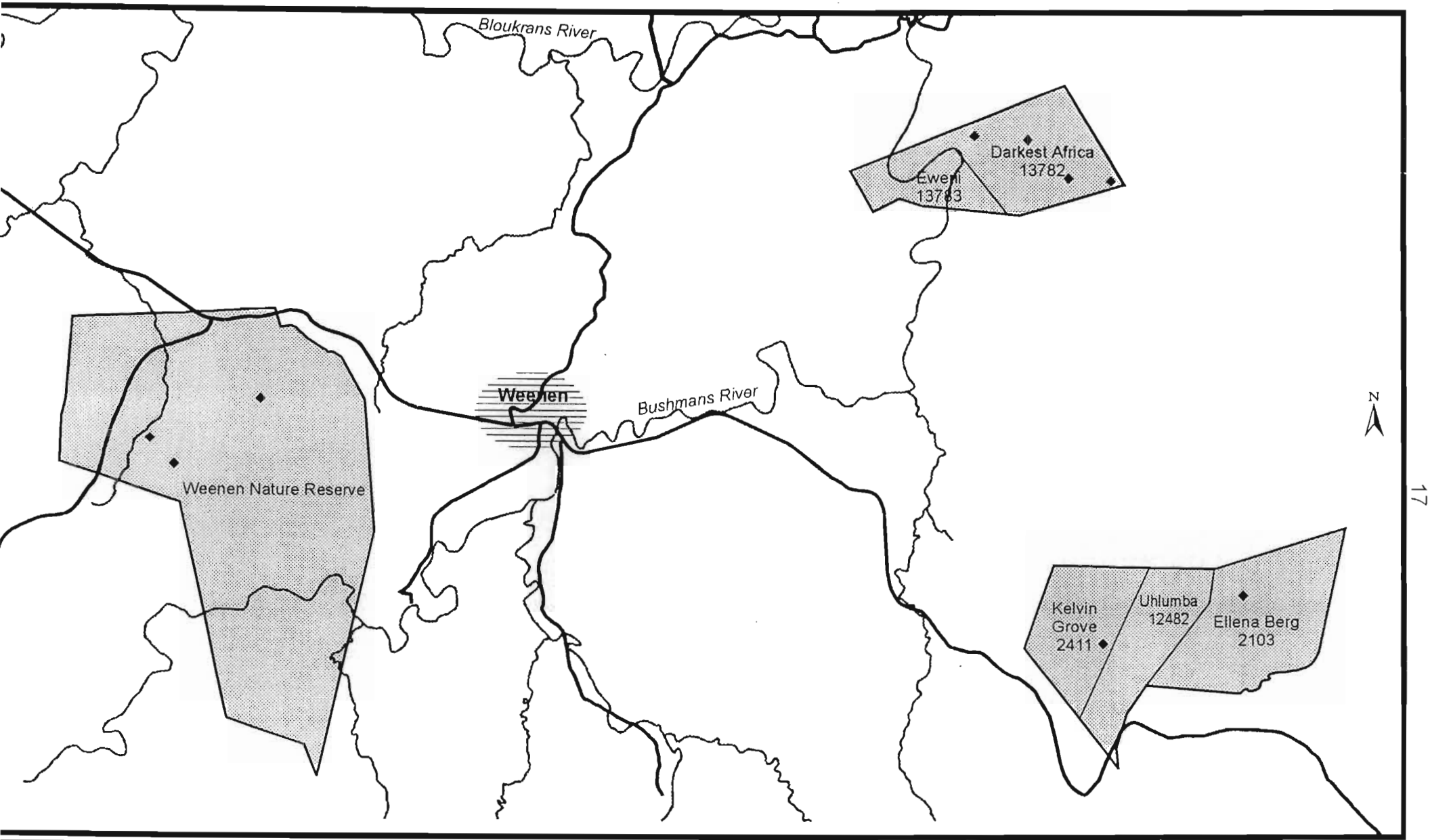

Figure 1.4 Location of Study Sites in the Weenen district, KwaZulu-Natal, South Africa

Located between 880 m and 940 m, the `Darkest Africa' (DA) study site is situated near the confluence of the Bushmans and Tugela Rivers (30°11'E 28°47'S). `Darkest Africa' was never a labour farm and has never been overgrazed (Opperman pers. comm.) so that very little degradation of the rangeland is apparent. The woody vegetation is dominated by semi-deciduous broadleaved shrubs and trees while the well-developed herbaceous layer is dominated by *Themeda triandra* **Forsk.**.

The Weenen (WE) study site is part of the Weenen Nature Reserve and is situated between 980 m and 1100 m on the Bushmans River, approximately 20 km upstream from "Darkest Africa" (30°02'E 28°52'S). Until 1952 the reserve was a labour farm after which it was taken over by the Department of Agriculture. Since then a programme of intensive rehabititation has been undertaken. First, stock were completely removed from the rangeland. Next, extensive stone and brush packings were done along contours and gullies were blocked to slow the rate of soil erosion. Finally, *T. triandra* was established by packing seed-bearing *T. triandra* `thatch' on bare ground and covering it with branches obtained by cutting down all the small woody plants in the vicinity of the site. Today, where *T. triandra* has been successfully established, fire is applied regularly to curb bush encroachment. However, in many places the herbaceous cover is still poor. The Natal Parks Board took over management of the reserve in 1975.

The reserve is 5000 ha in extent and is stocked with small numbers of various game species. Herbivores that occur in the reserve at present are white rhinoceros (*Ceratotherium simum* (**Burchell**)), black rhinoceros (*Diceros bicornis* (**L.**)), Cape buffalo (*Syncerus caffer* (**Sparrman**)), roan antelope (*Hippotragus equinus* (**Desmarest**)), kudu (*Tragelaphus strepsiceros* (**Pallas**)), red hartebeest (*Alcelaphus buselaphus* (**Pallas**)), eland (*Taurotragus oryx* (**Pallas**)), giraffe (*Giraffa camelopardalis* (**L.**)), plains zebra (*Equus burchelli* (**Gmelin**)), grey duiker (*Silvicapra grimmia* (**L.**)) and bushbuck (*Tragelaphus scriptus* (**Pallas**)). The woody vegetation is dominated by *A. nilotica* and *Acacia karroo* **Hayne**. In addition, semi-deciduous broadleaved shrubs and trees as well as succulent plants are abundant.

The Mhlumba (MHL) study site included the farms Ellena Berg and Kelvin Grove which are situated around the base of Mhlumba Mountain (30°15'E 28°53'S). This study site ranges in elevation from 1000 m to 1100 m. Both were previously

labour farms and were heavily utilised by subsistence farmers until 1980 (Gill pers. comm.). Severe degradation took place during this period and to date no intensive reclamation has been attempted. Both farms are still stocked with cattle. The woody vegetation is dominated by *A. karroo* and the herbaceous cover is extremely poor. These farms were reported to be the worst eroded lands in South Africa (Acocks 1953).

CHAPTER TWO: COMPOSITION AND STRUCTURE OF WOODY VEGETATION CLUSTERS AND WOODY VEGETATION BETWEEN CLUSTERS IN THE WEENEN DISTRICT

2.1 Field Sampling

The definition and field identification of woody vegetation clusters is difficult and often determined on the basis of the experience and objectives of the observer. In a similar study in Texas, a shrub cluster was defined as "...any association of two or more shrub species (including cacti) that have their combined canopies separated from other woody plants by a herbaceous clearing..." (Archer *et al* 1988). Edwards (1967) defined `bush clumps' in the Tugela Basin as "small dense communities composed of an aggregation of climbers, shrubs and small trees around one or two large trees". For the purpose of this study a bush cluster was defined as **a continuous woody plant canopy comprising more than one individual woody plant**. Vegetation clusters that satisfy this definition are easily identified in the Natal bushveld (Bews 1917, Comins 1953, Edwards 1967 & Moll 1971). This definition includes monospecific clusters in the sample, so that a wide range of potential interactions among individual plants, such as inter- and intraspecific competition and facilitation, are considered.

Compositional and size class data of the between bush cluster vegetation on rocky slopes were collected at Weenen and `Darkest Africa'. At the other study sites, with the exception of Maphumulo which is relatively undisturbed, it was obvious that owing to the intensive, recent exploitation by humans many individual trees actually represented remnant bush clusters (Camp 1986). Therefore, data on between-cluster vegetation composition were not collected at these sites. These data were collected at Weenen from 25 randomly placed 10 m X 10 m quadrats. All woody species present in these quadrats were identified and their heights measured. The means and standard errors for numbers of individuals per hectare for each species were calculated. A different sampling procedure was used at the later successional site, `Darkest Africa'. Here thirty-four 10 m wide transects of varying length were sampled. In each transect all individual woody plants were recorded by species and height class (<0.5 m, 0.5 m to <2 m and >2 m). The distance traversed along each transect to encounter 100

plants in the >2 m tall height class was recorded. Mean density and standard error for each species in the >2 m height class were calculated. This procedure was adopted due to the height of the grasses at `Darkest Africa', which made accurate estimates of the mean densities of the smaller height classes difficult.

Vegetation composition and height class data were collected for 150 bush clusters; 47 at the Weenen study site (WE), 50 at the `Darkest Africa' site (DA), 40 at the Mhlumba site (MHL), 10 near Keats Drift in the Msinga district (MS), and three in the Tugela Valley below Maphumulo (MAP). For each bush cluster all individual plants were recorded by species, stem diameter, crown diameter and height. An index of area covered by the bush cluster was calculated from measurements of the longest axis through the cluster and second longest axis at right angles to the first axis. Elevation, slope and aspect were recorded for all clusters. Bush clusters were sampled along 10 m wide and 100 m long randomly located transects to obtain an unbiased systematic collection of data. Within each transect all bush clusters inside or touching the transect were sampled. Transects ran across various obvious environmental gradients such as slope aspect and slope angle as well as elevation. This was done deliberately to see whether, even with such environmental variation, a general pattern of species distributions could be detected.

2.2 Analyses and results

2.2.1 Species composition of woody vegetation between bush clusters at Weenen and `Darkest Africa'.

Thirteen species of woody plants were recorded in quadrats located between bush clusters at Weenen (Table 2.1 next page).

Table 2.1 The mean number and relative frequency of woody species found between bush clumps at the Weenen study site. The standard deviation is given in parenthesis.

	Density / ha	Species Relative Frequency (%)
Euclea natalensis	676 (940)	19.2
Acacia nilotica	628 (470)	17.8
Acacia caffra	524 (760)	14.9
Vitex rehmanni	380 (300)	10.8
Maytenus heterophylla	340 (540)	9.7
Calpurnia aurea	308 (310)	8.7
Rhus pentheri	256 (230)	7.3
Rhus dentata	204 (150)	5.8
Brachylaena sp.	60 (90)	1.7
Ozoroa paniculosa	52 (120)	1.5
Rhoicissus tridentata	44 (110)	1.2
Ziziphus mucronata	36 (70)	1.0
Holmskioldia sp.	12 (40)	0.3

Four species, *Euclea natalensis* **A.DC.**, *Acacia nilotica*, *Acacia caffra* **(Thunb).Wild.**, and *Vitex rehmannii* **Gurke** comprised more than 60% of all individuals sampled. Three species, *Maytenus heterophylla* **(Ecklon & Zeyher) N.K.B. Robson**, *Calpurnia aurea* **(Ait.) Benth.** and *Rhus pentheri* **Zahlbr.** contribute an additional 25% to the number of individuals sampled. With the exception of *R. pentheri*, all of the common species decline in abundance from the shorter height classes to the taller (Table 2.2 next page). Twelve of the 13 species recorded between bush clusters were also recorded as members of the bush clusters.

Table 2.2. The number of individuals in each size class of woody species found between bush clumps at the Weenen study site. The percentage representation in each size class is given in parentheses.

	Species		
	<0.5 m	0.5-2 m	>2 m
Euclea natalensis	160	9	0
Acacia nilotica	122	28	4
Acacia caffra	109	19	0
Vitex rehmanni	52	43	0
Maytenus heterophylla	71	13	0
Calpurnia aurea	71	6	0
Rhus pentheri	25	38	0
Rhus dentata	29	25	0
Brachylaena sp.	9	6	0
Ozoroa paniculosa	10	4	0
Rhoicissus tridentata	10	1	0
Ziziphus mucronata	7	1	0
Holmskioldia sp.	3	0	0

Thirty-eight woody species were recorded in the `Darkest Africa' transects. Of these, 27 species were represented in the > 2m height class (Table 2.3 next page).

Table 2.3. The mean number and relative frequency of individuals > 2m high for woody species found between bush clumps at the `Darkest Africa' study site. The standard deviation is given in parentheses. The dash (-) indicates presence but with means and standard deviations less than one or contributing less than 1% to the total number of individuals recorded.

Species	Density (ha)	Relative Frequency (%)
vitex rehmanni	37 (29)	41.7
Aloe spectabilis	14 (15)	15.5
Acacia caffra	11 (13)	11.8
Acacia tortilis	10 (10)	11.6
Maytenus heterophylla	4 (8)	4.8
Tarchonanthus camphoratus	3 (6)	3.4
Combretum apiculatum	2 (6)	2.5
Grewia monticola	2 (4)	2.1
Grewia hexamita	1 (6)	1.5
Acacia nolitica	1(5)	1.4
Brachylaena eliptica	- (1)	0.5
Ozoroa paniculosa	- (1)	0.4
Rhus pentheri	- (1)	0.4
Ximenia caffra	- (1)	0.3
Dichrostachys cinerea	-	0.2
Dombeya cymosa	-	0.2
Euclea divinorum	-	0.2
Sclerocarya birrea	-	0.2
Zanthoxylum capense	-	0.2
Cussonia spicata	-	0.1
Premna mooiensis	-	0.1
Vepris lanceolata	-	0.1

Continued ...

Acacia ataxacantha	-	-
Acacia karroo	-	-
Ethretia rigida	-	-
Maytenus undata	-	-
Olea europaea	-	-

Four species, *V. rehmannii*, *Aloe spectabilis* **Reynolds**, *A. caffra* and *Acacia tortilis* **(Forsk) Hayne** accounted for more than 80% of all woody plants > 2m tall found outside bush clusters. Three species, *M. heterophylla*, *Tarchonanthus camphoratus* **L.** and *C. aurea*, contribute an additional 20% of the total number of individuals recorded between bush clusters. The other 31 species were relatively rare with 22 species contributing only 4.5% of the total number of individuals recorded outside bush clusters. All seven of the commonest species recorded in the open sites were also found in bush clusters. Thirteen of the species found outside bush clusters were not recorded in the samples taken from bush clusters.

2.2.2 Species composition of woody vegetation clusters

In the 150 vegetation clusters sampled, 2176 individual woody plants were recorded representing 84 species (Table 2.4).

Table 2.4. The relative commonness of woody species at different study sites. (Commonness expressed as a percentage of clusters in which a species occurred at each study site.) DAR = 'Darkest Africa', MSI = Msinga, MHL = Ellena Berg & Kelvin Grove, MAP = Maphumulo, WEE = Weenen, - = not present

Species	DAR	MSI	MHL	MAP	WEE	Total
Acacia nilotica	28	30	43	67	79	49
Rhus pentheri	52	-	5	100	62	40
Coddia rudis	56	60	45	-	15	39

Continued ...

Vitex rehmannii	70	80	-	-	32	39
Acacia karroo	6	-	75	33	40	35
Grewia occidentalis	54	20	30	67	4	30
Brachylaena elliptica	44	-	3	-	34	26
Acacia tortilis	24	50	30	-	15	24
Acacia caffra	44	-	3	33	21	23
Aloe spectabilis	40	60	8	-	-	19
Ozoroa paniculosa	24	10	-	-	32	19
Maytenus heterophylla	26	10	5	67	21	19
Maytenus senegalensis	32	-	18	-	-	15
Ehretia rigida	18	20	28	33	-	15
Cussonia spicata	20	-	-	67	21	15
Premna mooiensis	38	-	3	33	2	15
Berchemia zeyheri	38	-	5	-	-	14
Zanthoxylum capensis	36	-	-	67	-	13
Calpurnia aurea	4	20	-	-	32	13
Ziziphus mucronata	12	-	5	100	13	11
Calpurnia aurea	4	20	-	-	32	13
Ziziphus mucronata	12	-	5	100	13	11
Olea europaea	28	-	-	-	4	11
Schotia brachypetala	14	-	-	33	17	11
Canthium spp.	6	-	-	67	11	11
Euclea natalensis	12	-	-	67	17	11
Rhus dentata	8	-	5	-	19	10
Pappea capensis	20	-	5	33	2	9
Vepris natalensis	22	10	-	67	-	9
Acacia robusta	8	-	8	33	11	9
Blepharis natalensis	-	-	30	-	-	8
Euclea racemosa	14	-	3	-	6	7

Continued ...

Euphorbia ingens	6	10	-	-	15	7
Grewia monticola	20	-	-	-	-	7
Euclea schimperi	14	-	3	33	-	6
Maytenus undata	16	10	-	-	-	6
Rhoicissus tridentata	-	-	-	-	17	5
Tarchonanthus camphoratus	-	-	-	-	13	5
Phyllica paniculosa	14	-	-	-	-	5
Ptaeroxylon obliquum	12	-	-	33	-	5
Clerodendrum glabrum	-	10	-	-	11	4
Cussonia natalensis	12	-	-	-	-	4
Boscia albitrunca	2	-	13	-	-	4
Acacia ataxacantha	6	-	-	67	-	3
Dead	6	-	3	33	-	3
Prostasperagus spp.	-	-	3	-	6	3
Scolopia zeyheri	4	4	5	-	5	3
Celtis africana	6	-	-	33	-	3
Ximenia caffra	-	-	-	-	9	3
Cassine transvaalensis	8	-	-	-	-	3
Rhus rhemanniana	4	-	-	-	4	3
Chaetacme aristata	-	-	-	100	-	2
Dichrostachys cinerea	-	-	-	33	4	2
Commiphora wooddii	4	-	-	33	-	2
Trimeria grandifolia	-	-	-	100	-	2
Sideroxylon inerme	2	-	-	67	-	2
Diospyros lycioides	-	-	-	33	4	2
Canthium obovatum	-	-	-	100	-	2
Monanthotaxus natalensis	-	-	-	67	-	1
Euclea divinorum	-	-	-	67	-	1
Rapanea melanophoeos	-	-	-	67	-	1

Continued ...

Combretum molle	-	-	-	67	-	1
Combretum apiculatum	-	4	-	-	-	1
Dombeya cymosa	-	2	-	-	2	1
Dalbergia armata	-	-	-	33	2	1
Vangueria infausta	-	-	-	67	-	1
Dais continifolia	-	-	-	-	4	1
Hippobromus pauciflora	-	4	-	-	-	1
Opuntia ficus-indica	-	-	20	-	-	1
Dombeya rotundifolia	-	-	-	33	-	1
Scutia myrtina	-	-	3	-	-	1
Rhus tomentosa	-	-	-	33	-	1
Commiphora harveyi	-	-	-	33	-	1
Ficus natalensis	-	-	-	33	-	1
Quisqualis parviflora	-	-	-	33	-	1
Euphorbia tirucalli	-	2	-	-	-	1
Schrebera alata	-	-	3	-	-	1
Euclea crispa	-	-	-	-	2	1
Acokanthera oppositifolia	-	2	-	-	-	1
Acacia sieberiana	-	-	-	-	2	1
Tecomaria capensis	-	-	-	33	-	1
Ochna spp.	-	-	-	33	-	1
Sclerocarya birrea	-	2	-	-	-	1
Combretum kraussii	-	-	-	33	-	1
Dalbergia obovata	-	-	-	33	-	1

Dead plants, often occurring as large stumps, which could not be identified to species level were treated as an additional species. Judging from their size, wood structure, and in some cases bark, most of these dead individuals were either *A. nilotica* or *A. caffra*.

Four species, *Euphorbia tirrucali, E. ingens, A. spectabilis* and *Opuntia ficus-indica* **(L.)** are succulent arborescent plants. Five species, *Rhoicissus tridentata* **(L.F.)Wild & R.B.Drumm**, *Protasparagus* sp., *Dalbergia armata* **E. Meyer**, *D. obovata* **E. Meyer**, *Scutia myrtina* **(N.L.Burn)Kurz** and *Acacia ataxacantha* **DC.**, are creepers. Two species, *Blepharis natalensis* **Oberm.** and *Coddia rudis* **E. Meyer ex Harv. Codd**, are dwarf shrubs and rarely exceeded 1 m in height. The remaining species may all grow taller than 3 m (Coates Palgrave 1983). When data from all the study sites are combined, 12 species accounted for 62% of the plants recorded.

Vegetation clusters tended to be multispecific and frequently comprised of plants from more than one height and stem diameter class. Marked differences in species composition, area and species richness of woody vegetation clusters of the different study sites occurred (Table 2.5).

The most species-rich site is Maphumulo where three clusters comprising 208 plants represented 47 species. Overall, the species richness of clusters at this site varied from 11 to 40 species per cluster.

At `Darkest Africa', 897 plants representing 57 species were recorded in 50 clusters. The mean species richness of these clusters was 10 species, and varied from two to 24 species per cluster. Twenty species, *A. nilotica* (28%), *R. pentheri* (52%), *C. rudis* (56%), *V. rehmannii* (70%), *Grewia occidentalis* **L.** (54%), *Brachyleana eliptica* **(Thunb.) Less.** (44%), *A. tortilis* (24%), *A. caffra* (44%), *A. spectabilis* (40%), *Ozoroa paniculosa* **(Sonder) R. & A Fernandes** (24%), *M. heterophylla* (26%), *M. senegalensis* **(Lam.) Exell** (32%), *Cussonia spicata* **Thunb.** (20%), *Premna mooiensis* **(H.H.W. Pearson) Pieper** (38%), *Berchemia zeyheri* **(Sonder) Grubov** (38%), *Zanthoxylum capense* **(Thunb.) Harv.** (36%), *Olea europaea* **L.** (28%), *Pappea capensis* **Ecklon & Zeyher** (20%), *Vepris undulata* **(Thunb.) Verdoorn & C.A. Smith** (22%) and *Grewia monticola* **Sonder** (20%) occurred in ten or more of the clusters. Eleven species accounted for 60% of all the woody plants recorded.

At Weenen, 584 individual woody plants were recorded with 38 species occurring in the 47 clusters sampled. Twelve species, namely *A.nilotica* (79%), *R. pentherii* (62%), *C. aurea* (32%), *V. rehmannii* (32%), *B. eliptica* (34%), *A. caffra* (21%), *O. paniculosa* (32%), *M. heterophylla* (21%), *C. spicata* (21%) and *Acacia karroo* (40%)

occurred in 20% or more of the clusters. The mean species richness of vegetation clusters was six species and varied from two to 16 species per cluster. Five species accounted for 60% of the woody plants recorded.

At Mhlumba, 432 individual woody plants representing 27 species were recorded in 40 clusters. The mean cluster species richness was four species and varied from 1 to 6 species. Only seven species, namely *A. nilotica* (43%), *C. rudis* (45%), *A. karroo* (75%), *G. occidentalis* (30%) and *Ehretia rigida* **Thunb.) Druce** (28%) occurred in 20% or more of the clusters. Four species accounted for 60% of all the woody plants recorded.

In the Msinga District 72 individual woody plants representing 15 species were recorded in ten clusters. Mean cluster species richness was four species and varied from one to six species. Only nine species, *A. nilotica* (30%), *C. rudis* (60%), *V. rehmannii* (80%), *G. occidentalis* (20%), *A. tortilis* (50%), *A. spectabilis* (60%), *E. rigida* (20%), *C. aurea* (20%) and *O. ficus-indica* (20%) occurred in 20% or more of the clusters.

2.2.3 Shape of woody vegetation clusters and cluster area index

An index of cluster area was calculated as the surface area of a circle where cluster area = (mean axis length ÷ 2)^2 x 3.1416. At 'Darkest Africa' the mean cluster area index was 82.1 m^2 and varied from 7.1 m^2 to 311 m^2. Mean cluster area index at Weenen was 69.13 m^2 and varied from 4.52 m^2 to 219.64 m^2. At the Mhlumba sites the mean cluster area index was 12.42 m^2 and varied from 1.77 m^2 to 35.79 m^2, while at the Msinga site the mean was 5.48 m^2 and varied from 0.79 m^2 to 19.64 m^2. No mean cluster area was calculated for the Maphumulo site as only three large clusters were sampled there.

The difference in the length of the perpendicular axes of a cluster describes cluster shape. If there is only a small difference, then the cluster is roughly circular. The mean difference for 150 clusters was 2.86 m, which represents only 0.19% and 0.23% of the mean long and its longest perpendicular axis lengths respectively. A difference greater than 2 m between the two cluster axes was chosen arbitrarily to indicate departure from circularity. Generally, it would appear that smaller clusters are roughly

regression of the difference in length of cluster axes (Y) on cluster area index (X) showed a strong positive relationship (Figure 2.1; n = 150, Y = 0.03X + 0.29, r^2 = 0.654, $P << 0.001$). There is no consistent orientation in relation to slope or aspect for non-circular clusters.

It seems that two growth phases exist in cluster development. An (i) initial phase of concentric expansion of the cluster perimeter and then (ii) a later stage of random expansion. Thus growth of the bush cluster during the first phase is due to size increases of individual plants in the cluster and also to recruitment of new plants at its edge. In the second phase, growth is mainly due to coalescence of two or more clusters.

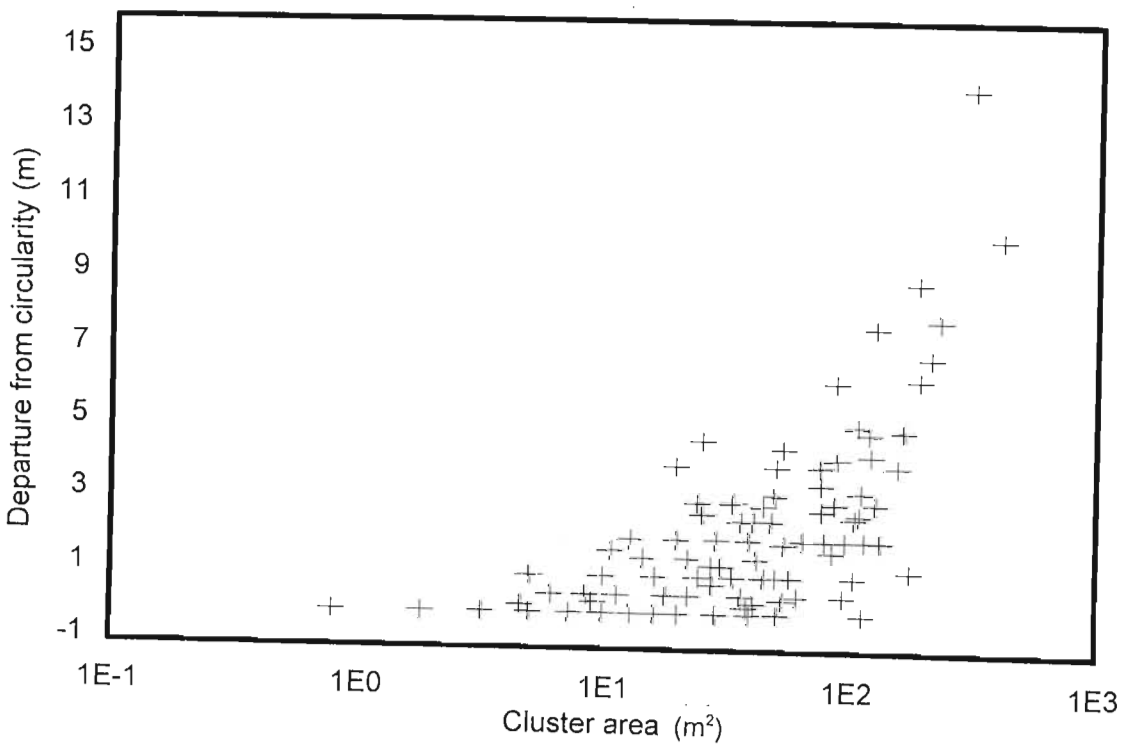

Figure 2.1. The relationship between cluster area and cluster shape. (Arbitarily departure from circularity is expressed as a difference of more than 2 m between two longest perpendicular cluster axes.)

2.2.4 Species richness and diversity of clusters

The relationship developed by Preston (1962), $S = cA^z$, where species richness (S) is an exponential function of cluster area in square meters (A) was used to generate a species-area curve for the data from all 150 clusters. The slope of the line relating S and A is given by z, while c represents the Y intercept. The $\log_{10}$ of A is regressed on $\log_{10}S$ to generate c and z.

The expected relationship between species richness and cluster area index when fitting the data for the 150 clusters to the Preston (1962) function is shown in Figure 2.2, where $c = 0.2534$ and $z = 0.362$, $r^2 = 0.49$. The observed relationship is shown in Figure 2.3.

Diversity was estimated using $exp(H')$, where $H' = \sum p_i lnp_i$, and p_i was the relative canopy area of species in a cluster. The term $Exp(H')$ was used rather than H' because the former represents the number of equally common species in a sample (Peet 1974). Evenness (E) was estimated using Alotalo's (1981) variation of Hill's (1979) ratio:

$E = (N_2 - 1) / (N_1 - 1)$, where $N_2 = 1/\sum p_i^2$ and $N_1 = exp(H')^2$.

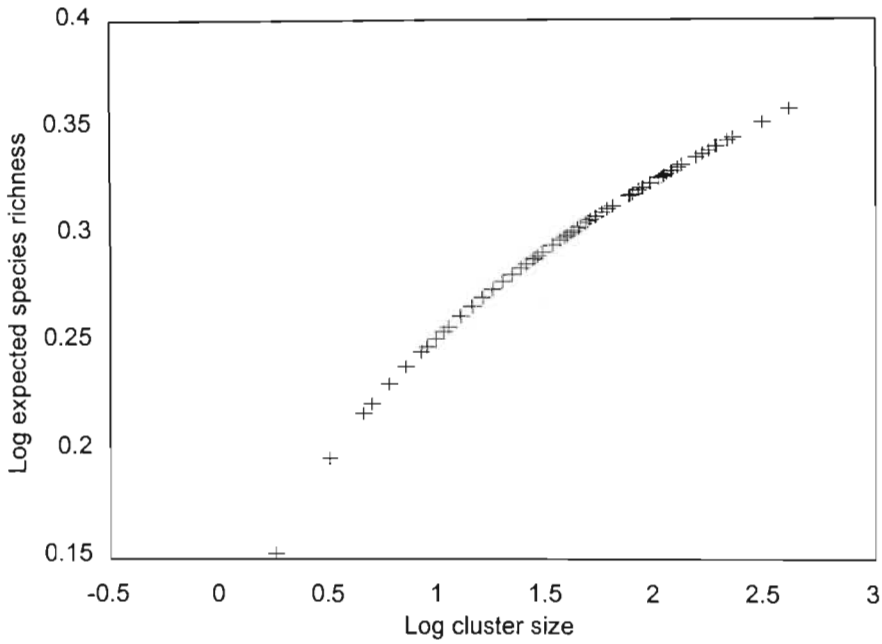

Figure 2.2. Expected species/area curve for 150 bush clusters in the Weenen District as predicted by the Preston (1962) relationship.

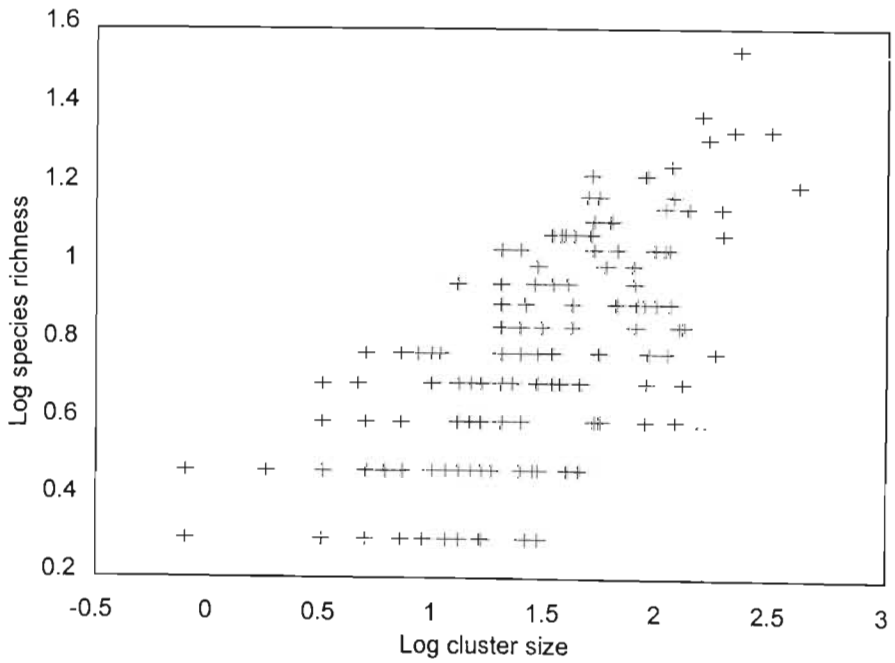

Figure 2.3. The observed relationship between species richness and cluster area for 150 bush clusters.

Table 2.5 shows the relationship between area index and species richness, diversity index and evenness of the 50 clusters from the `Darkest Africa' study site. The relationship between species diversity of bush clusters and cluster area is approaching significance at the $P < 0.05$ level. This is likely to be the result of only one or two large individual plants usually accounting for the largest proportion of cover in most of the bigger clusters. Species evenness and species richness are positively and significantly correlated to bush cluster area.

Table 2.5. The relationship between the index of bush cluster area (X) on species diversity, evenness and richness.

	n	Equation	r	*P*
Diversity	50	Y = 0.003x + 1.25	0.28	0.1 < *P* < 0.05
Evenness	50	Y = 0.10x + 1.59	0.71	<< 0.001
Richness	150	Y = 0.07x + 6.16	0.77	<< 0.001

2.3. Discussion

The observed relationship between cluster species richness and cluster area index (Figure 2.3) is consistent with the results obtained by Archer *et al* (1988) in the mesquite-woodlands of Texas. It also approximates the Preston (1962) relationship (Figure 2.2). This significant relationship ($r^2 = 0.49$), suggests that cluster area can be used to predict species richness. For the purpose of a `space-for-time substitution model', cluster area is used as an indicator of cluster age in terms of `successional time' (Archer *et al* 1988). It can be argued that cluster species richness and species composition are less likely to reflect the influences of disturbance factors such as drought, fire, herbivory or exploitation of woody plants by man, than will cluster area (Archer 1990). Large monospecific clusters are also frequently observed in the Natal bushveld on abandoned croplands. Such monospecific clusters are generally closed-canopy thickets of woody plants such as *Dichrostachys cinerea* **(L.) Wight & Arn.**, *A. nilotica, A.karroo* or *A.tortilis* (personal observation). In the case of such monospecific clusters, cluster area does not reflect successional status. It is therefore suggested that

species richness should be used as an indication of the developmental status of clusters rather than cluster area. In addition, species richness is an explicit value that can easily be obtained by counting the number of species in a cluster, while cluster area is difficult and time consuming to measure accurately and, at best, only an index can be calculated. Also the cluster area index is misleading as it reflects the intense exploitation of wood resources by subsistence farmers at the Msinga site and the effect of past exploitation as well as a possible earlier stage of bushveld development at higher elevations at the Mhlumba and Weenen sites.

Larger clusters tend to be non-circular in shape but there does not seem to be any significant relationship between the direction of cluster elongation and slope direction. This suggests that after an initial phase of individual growth, increase in cluster area is likely to occur as a result of coalescence between two or more individual clusters, and not by the concentric expansion of individual cluster perimeters. It can thus be expected that the rate of cluster growth at the landscape scale will be a result of the density of smaller clusters, or individual trees which might initiate the formation of new clusters under their canopies. In this case the availability of seeds to establish new clusters and the absence of events that prevent cluster formation are the key factors that influence bushveld development.

Although individual plants from 38 species were encountered outside woody vegetation clusters at `Darkest Africa, only four species co-dominated (>80% of individuals recorded) this vegetation phase. On the same study site, 50 species were recorded inside woody vegetation clusters, while eleven species co-dominated (>60% of individuals recorded) in the cluster phase. The cluster phase is thus not only more species rich, but also more diverse. It is clear that many of the woody species that occur in the Natal bushveld are dependant on the clustered structure of the vegetation for establishment and survival. Plants in clusters are more likely to be protected from fire and herbivory than are isolated individuals in the surrounding grassland. Only a few species seem to be able to maintain large populations outside bush clusters. It is suggested that, at the landscape scale, the cluster phase is important for the maintenance of species diversity and ultimately for the degree of ecosystem resilience.

It can be expected that in extremely variable physical environments only opportunistic or generalist species will be able to establish, survive and reproduce (Grime 1979, Begon *et al.* 1986). Thus, in an ecosystem with such an extremely variable rainfall as the Natal bushveld, the clustered structure of woody vegetation communities provides a buffer against variable environmental factors which otherwise will result in variable resource availability and survival potential of plants. In bushveld areas with a poorly developed cluster phase or where the cluster phase has been destroyed through intense utilisation of wood resources or by bush- clearing operations, lower species richness and diversity should occur. Such areas will be more `fragile' than areas where the cluster phase is well developed.

The results of this study support the above pattern, with species richness of study sites decreasing with decreasing mean cluster area and mean cluster species richness. The `Darkest Africa' site, where no severe degradation of the cluster phase is evident, had the largest mean cluster area index (82.1 m^2) and cluster species richness (10). It was the most species rich of the sites (50), eleven species represent 60% of the recorded plants and 20 species occurred in 20% or more of the clusters.

The Weenen site, that had been severely degraded and then rehabilitated, had a smaller mean cluster area index (69.13 m^2) and a much lower mean cluster species richness (6) than the `Darkest Africa' site. This site was also less species rich (38); only five species represent 60% of the recorded plants and only 12 species occurred in more than 20% of the clusters.

The Mhlumba site, which has been severely degraded and never rehabilitated, had the lowest mean cluster area index (12.45 m^2) and the lowest mean cluster species richness four species. At this site these four species represent 60% of all the recorded plants and only seven species occurred in more than 20% of the clusters.

In conclusion:

- Cluster species richness can be used as a index of cluster developmental stage.
- Cluster growth is dependent on the rate at which different clusters can coalesce, and not concentric expansion of individual cluster perimeters. This, in turn, is dependent on the rate of cluster formation and survival.

- Most of the species that occur in the Natal bushveld seem to be dependent on the clustered structure of woody vegetation for establishment and survival.
- The effect of land-use practices which destroy the cluster phase of bushveld vegetation may (i) result in local extinction of species and loss of ecosystem resilience and (ii) retard the development of bushveld.
- The cluster phase in bushveld vegetation is important for the maintenance of species diversity and ecosystem resilience at the landscape scale.

CHAPTER THREE: PATTERNS IN WOODY VEGETATION CLUSTER STRUCTURE IN RELATIONSHIP TO ENVIRONMENTAL GRADIENTS

3.1. Introduction

All species occur in a characteristic, limited range of habitats and within this range, tend to be most abundant around a particular environmental optimum. The composition of biotic communities therefore changes along environmental gradients. Successive replacement of species occurs as a function of variation in the environment, or (analogously) with successional time (Picket 1980, Peet & Loucks 1977). The concept of niche partitioning also implies the separation of species along `resource gradients' (Tilman 1980, 1982). Gradients do not necessarily have physical reality as continua in either space or time but may be a useful abstraction for explaining the distributions of organisms (Austin 1985).

Use of the word `gradient' introduces the central theme in an approach to analysing vegetation data known as ordination. Classification of data into discrete categories is regarded as the complementary strategy to ordination. The term "ordination" refers to a range of approaches which have been developed to order (*i.e.* arrange) samples of vegetation data into some pattern which can be related to one or more environmental variables. All ordination methods aim to depict the gradient of greatest variation along the 'first' axis, the second largest gradient along the 'second' axis, and so on. Axes higher than the 'third' are generally less useful because not only do they contain progressively less information, but they often cause distortion on these lower axes (Gauch 1982).

Gradient analysis is the study of spatial patterns of vegetation in relation to underlying environmental gradients using ordination (Whittaker 1967 & Krebs 1972). Two basic types of gradient analysis are recognised. In direct gradient analysis (DGA) sites and species are arranged according to their relative positions along measured enviromental gradients such as altitude, soil pH, etc. Environmental variables used for analysis, and which form the axes of the ordination, are selected subjectively on the assumption that they are important in controlling the distribution of the plant species under consideration. One, two, and sometimes three, individual environmental variables are used to form the axes of the ordination. Because DGA often involves the

simultaneous use of two or three variables, regression analysis is often used to fit lines or surfaces to the data in order to describe more precisely the extent to which the variables under consideration are correlated. The most severe limitation of DGA is the limited number of environmental factors that can be examined in a single analysis.

In the alternative approach, known as indirect gradient analysis (IGA), mathematical procedures are used to order samples and/or species along axes which seek to describe the variation in floristic composition. Thus IGA is based on vegetation data. Because the axes are constructed without reference to environmental measurements they may be termed latent variables or hypothetical environmental gradients which have been constructed in such a way as to optimise the fit of the species data to a particular linear statistical model which best describes the variation of the species abundance along some gradient (ter Braak 1985, 1987, ter Braak & Prentice 1988). Once having been identified the axes can then be interpreted in the light of either measured or nominal environmental gradients (Whittaker 1967). Thus, in IGA, relationships between species gradients and environmental gradients is inferred whereas in DGA relationships between species are determined by each species' response to a particular environmental variable. Like DGA, IGA techniques make use of two or three axes to graphically illustrate in two or three dimensions these relationships. Typically, IGA techniques are designed to analyse many factors in a single analysis and a close relationship exists among the various techniques (Austin 1971).

Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980) is an indirect ordination technique that is a modification of Correspondence Analysis (CA). Correspondence Analysis usually makes use of the algorithm known as Reciprocal Averaging (Hill 1973, 1974 & 1979a). However, this has two conspicuous faults which are that site scores along a particular ordination axis often show a quadratic relationship with those of the preceding axis resulting in the so-called "arch effect" (Hill & Gaugh 1980) and that scores for sites which occur towards the tails of the ordination axes are compressed relative to those near the middle of the axes. Detrended Correspondence Analysis employs certain mathematical manipulations which include detrending and nonlinear rescaling of site scores to correct these problems (Hill & Gaugh 1980, ter Braak 1966).

Detrended Correspondence Analysis works remarkably well in practice to solve ordination problems (Gauch *et al* 1981). It has also been critically evaluated in several simulation studies. ter Braak (1985) showed that DCA gave a close proximation of Gaussian ordination when applied to simulated data based on a two-dimensional species packing model in which species have identically shaped Gaussian surfaces and the optima and site scores uniformly distributed in a rectangle. For these reasons DCA is popular among practical field ecologists and has been used extensively in ecological applications (Kent & Ballard 1988).

Archer *et al* (1988), working in mesquite woodland in Texas, reported the existence of a strong temporal cluster development gradient in which cluster area, species richness, and the distribution of individual species could be correlated with the passage of time. This gradient was detected using DCA ordination of octave transformed species cover data from 56 bush clusters. In this study, Axes I and II accounted for 49.8% and 22.0% of the variation respectively. When the species richnesses of the clusters were plotted on the coordinates of the axis scores, it became clear that Axis I represented a `succession gradient' which could be described by the species richness of the clusters.

Field observations suggested that a similar pattern existed in the Natal bushveld. However, it appears that the study site used by Archer *et al* (1988) represents a system which is simpler than the bushveld of the Weenen District. For example, they recorded only 20 woody species were in 56 clusters in contrast to the 38 species recorded in 47 clusters at Weenen in this study. Whittaker *et al* (1970) and Archer *et al* (1988) stated that mesquite (*Prosopis glandulosa* (**Torr**) var. *glandulosa*), was the most common leguminous pioneer woody species in the dense thorn woodlands of the Rio Grande Plains. Bush clusters of the Natal thorny bushveld are much more species rich (Chapter 2) but resemble those of Texas in that three leguminous species, *Acacia nilotica, A.karroo* and *A.tortilis* act as pioneers (Bews 1917, Comins 1953, Hurt 1993).

3.2. Methods

Indirect gradient analyses (ter Braak & Prentice 1988) were applied to investigate the possible existence of gradients that regulate the distribution of woody species in the Weenen District. To make direct comparisons with the dynamics of the woody vegetation reported by Archer *et al* (1988) and to reduce variation, it was neccessry to reduce the complexity of the data set. This was accomplished in several ways. Firstly, only species that had the potential to become canopy trees were included. Secondly, to reduce variation between samples, species represented in less than 2% of the clusters were omitted from the data set. Thirdly, because of their perceived functional similarity (Hurt 1993), the three early successional *Acacia* species, namely: *A.nilotica, A.karroo* and *A.tortilis* were treated as a single species. Fourthly, only clusters in which either *A. nilotica, A. karroo* or *A. tortilis* or a combination of these species occurred were included. This was done to eliminate bushclumps that may have been initiated by direct anthropogenic intervention, such as abandoned kraal sites which may have been planted with various non-leguminous species when occupied in the past. Finally, because of the severe disturbance of woody vegetation which still occurs in the Msinga and Maphumulo areas as a consequence of subsistence farming, the clusters from thees two areas were also omitted from the analysis. All the remaining clusters (n = 113), which came from `Darkest Africa', Weenen and Mhlumba were then ordinated after first summarising the data using the same methods described by Archer *et al* (1988).

Thus, canopy area was calculated for each individual plant in a cluster and then summed by species for that cluster and transformed to an octave scale for multivariate analysis. Detrended Correspondence Analysis was then carried out using the computer program DECORANA (Hill 1979). In order to detect the possible influence of site factors such as overgrazing and elevation, a second ordination was performed on only those clusters clusters which were sampled at `Darkest Africa' (n = 32), which was the least disturbed site.

3.3. Results and discussion

In the ordination of data set derived from clusters sampled at `Darkest Africa', Weenen and Mhlumba, the first two axes accounted for 36% and 29% of the variance respectively (Appendix Table 1). When the site names are superimposed on the co-ordinates generated by DCA for Axis I and II, the first axis appears to represent either a land-use or an altitudinal gradient, separating the clusters by site (Figure 3.1). The large degree of overlap (similarity) between the Weenen and `Darkest Africa' bush clusters suggests that the first axis most likely represents a gradient of land-use effects on the vegetation and not changes in the physical environment.

When the species richness values for the various clusters are superimposed on the co-ordinates generated by DCA for Axis I and II, it appears that Axis II represents a gradient that describes species richness (Figure 3.2). This is supported by the significant (R^2 = 0.22) relationship obtained by regressing (Table 3.1) cluster species richness on the second axis scores. This relationship is shown in Figure 3.3. As species richness is a function of area occupied by the cluster, and thus a function of the level of development of the cluster, this variant can be explained as a cluster development or `successional' gradient. These results show a similar trend to results described by Archer *et al* (1988). However, unlike their results, DCA in this study was did not group clusters into discrete groups based on their species richness.

In the case of the 32 bushclumps sampled at `Darkest Africa', ordination of these data yielded a first and second ordination axes which account for 34% and 19% of the variance respectively (Appendix Table 2). The first axis represents a gradient of cluster development or "successional gradient" (Figure 3.4). Regression of cluster species richness of the clusters on first axis scores shows a significant (R^2 = 0.39) relationship (Table 3.2). This relationship is shown in Figure 3.5. Again this is a trend which is similar to that described by Archer *et al* (1988), although no discrete groups were identified on the basis of species richness of the various clumps. There is, however, a clear continuum of increasing species richness in the clumps sampled. This means that a `successional' gradient accounts for nearly a third of the variation observed in the distribution of species populations in Natal bushveld. It is remarkable that even with

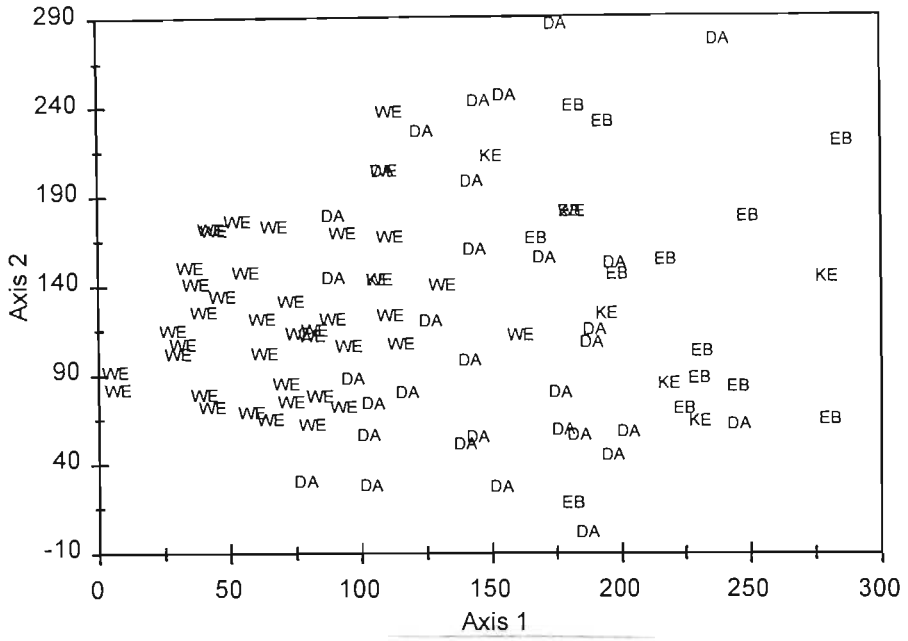

Figure 3.1. Scatter diagram of DCA output for 113 clusters from the 'Darkest Africa', Weenen and Mhlumba study sites, showing site names at the co-ordinates of the Axis scores. Axis I accounted for 36% and Axis II for 29% of the variation. The large degree of overlap suggests that it is possible a land-use effect and not a physical environmental gradient.

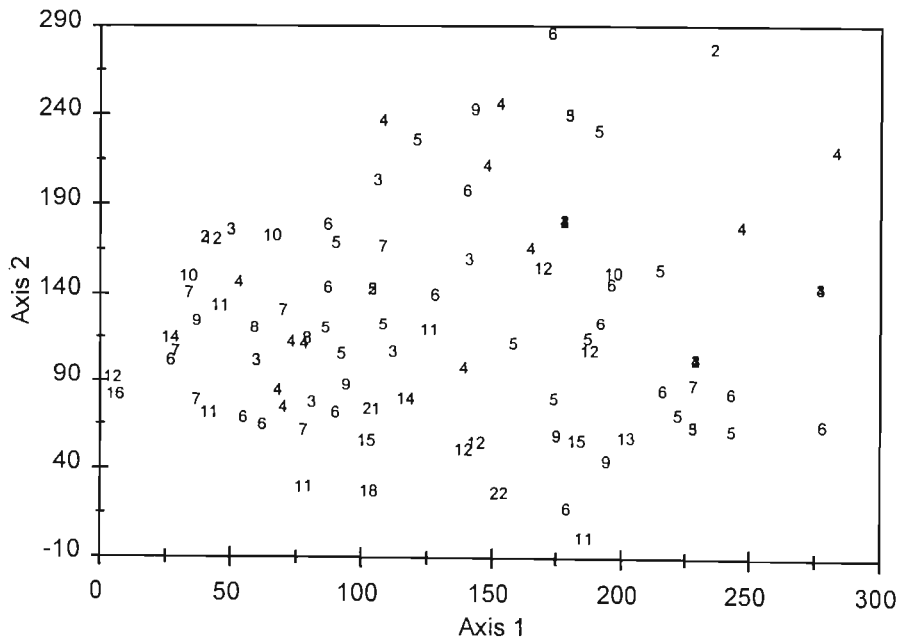

Figure 3.2. The relationship between cluster species richness and the scores of the second DCA axis for 113 bush clusters from the 'Darkest Africa', Weenen and Mhlumba study sites.

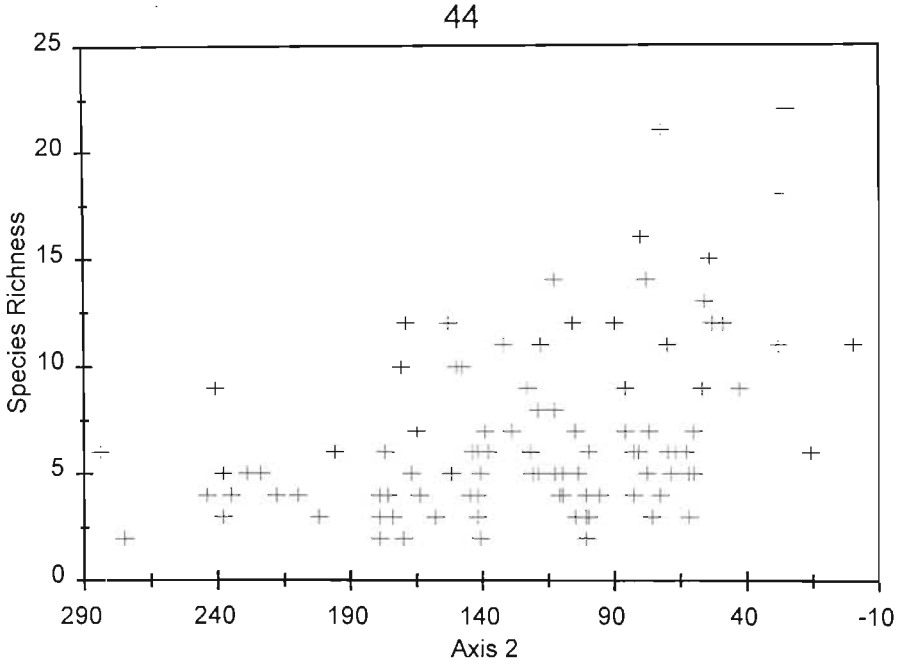

Figure 3.3. Scatter diagram of DCA output for 113 clusters from the 'Darkest Africa', Weenen and Mhlumba study sites, showing cluster species richness at the co-ordinates of the Axis scores. Axis I accounted for 36% and Axis II for 29% of the variation. The second axis represents a continuum of cluster species richness.

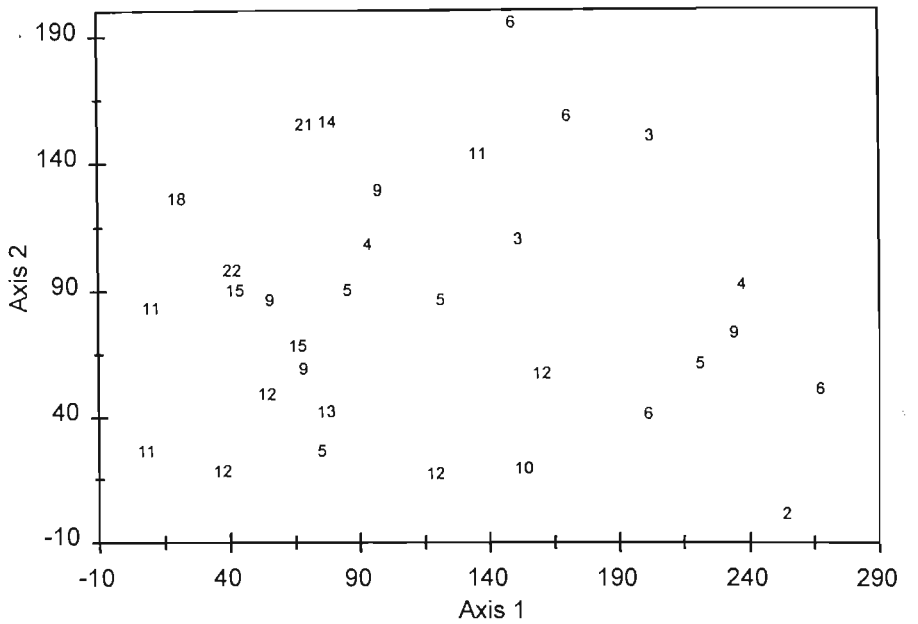

Figure 3.4. Scatter diagram of DCA output for bush clusters from the 'Darkest Africa' study site, showing cluster species richness at the co-ordinates of the axis acores. Axis I accounted for 34% and Axis II for 19% of the variance. The first axis represents a continuum of changing cluster species richness. This continuum can be described as a 'succession gradient' (Archer *et al.* 1988).

Table 3.1 Regression of species richness on the 2nd axis DCA scores for 113 clusters from the WE, DA and MHL study sites

Y	Y	R^2	*n*	DF	*X*	*X*
intercept	std				coefficient	std
10.53	3.68	0.22	113	111	-0.033	0.006

Table 3.2. Regression of species richness on the first axis DCA scores for 32 clusters from the DA study site

Y	Y	R^2	*n*	DF	*X*	*X*
intercept	std				coefficient	std
14.22	4.07	0.39	32	30	-0.042	0.0096

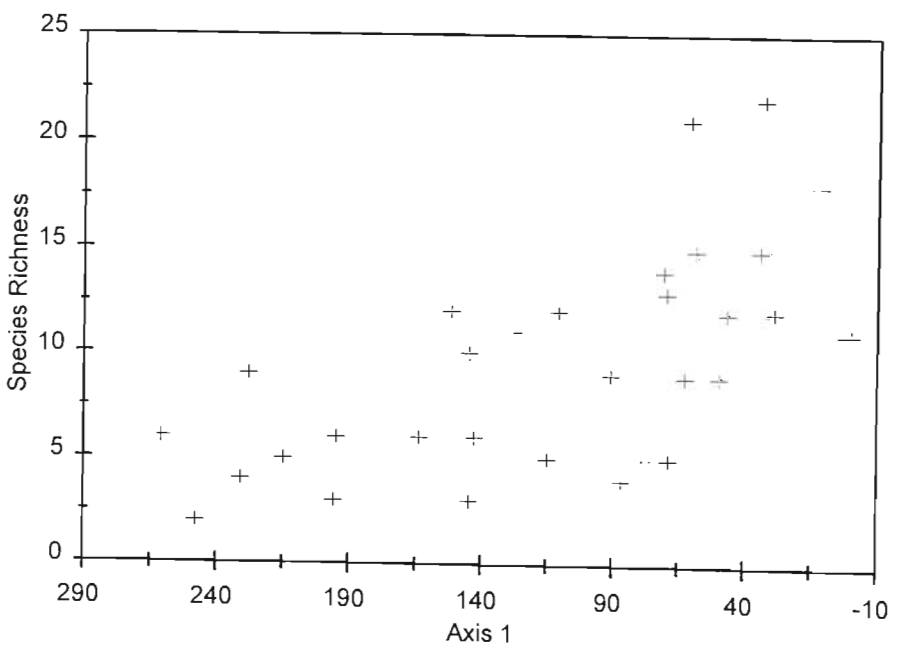

Figure 3.5. The observed relationship between cluster species richness and the scores of the first axis of DCA for 32 clusters from the 'Darkest Africa' study site.

the inclusion of other environmental variables, such as slope gradient, aspect and soil type, the `succession gradient' still accounts for such a large amount of the observed variation. However, the type of land-use and the intensity of natural resource exploitation is likely to be a stronger determinant of species distribution.

This observation supports the assumption that the distribution of individual plants is not governed solely by gradients in the physical factors that make up the environment (Van Hulst 1980), and that the effects of the physical factors are often masked by biotic interaction among individual plants (Nott 1991). In addition, these results also justify the use of the species richness of clusters as a parameter to describe a continuum of successional development. For modelling purposes such stages can be classified as discrete Clementsian successional stages namely early, mid-, and late succession.

To illustrate that a `successional gradient' can indeed be described by the species richness of bushclumps, it was hypothesised that a continuum of species composition turn-over, in which the number of species increases along the gradient, could be constructed. Analysis of variance (ANOVA) was therefore applied to test for the presence of significant differences in the numbers of individuals of the various species which determined the species richness of the various clusters (Table 3.3). When these ranges, expressed as the 90% confidence interval on the mean, are plotted along a gradient of increasing species richness of the clusters, species turnover along the gradient is apparent (Figure 3.6).

This successional species turn-over model not only confirms successional pathways suggested by earlier descriptive studies of the Natal bushveld (Bews 1917, Comins 1953, Killick 1959, Edwards 1967, Wells 1969 and Morris 1967). but also provides a more objective basis for successional classification of plant communities and woody plant species in the Natal bushveld. It confirms too, the general early invasion by leguminous, microphyllous, woody species followed by succulent or broadleaved woody plant species or both (Bews 1917; Brown & Archer 1989; Archer *et al* 1988; Archer 1989, 1990; Briers & La Cock 1991; Ben-Shahar 1991). It further suggests that both facilitation and competition act as mechanisms of plant succession in the woody communities of the Natal bushveld.

Table 3.3. Sample size and significance of response to a succession gradient of 45 woody species from the Weenen District.

Species	n	Response
Acacia ataxacantha	8	P < 0.001
Acacia caffra	42	P < 0.05
Acacia karroo	115	P < 0.001
Acacia nilotica	205	P < 0.001
Acacia robusta	23	P < 0.005
Acacia tortilis	75	P < 0.02
Aloe spectabilis	29	P < 0.001
Berchemia zeyheri	37	P < 0.001
Boscia albitrunca	8	No significance
Brachylaena elliptica	68	P < 0.001
Calpurnia aurea	74	P < 0.001
Canthium spp.	47	P < 0.001
Cassine transvaalensis	6	P < 0.02
Celtis africana	13	P < 0.001
Chaetacme aristata	12	P < 0.001
Clerodendrum glabrum	7	No significance
Cussonia natalensis	7	P < 0.005
Cussonia spicata	36	P < 0.001
Ehretia rigida	36	P < 0.05
Euclea natalensis	41	P < 0.001
Euclea racemosa zuluensis	14	P < 0.02
Euclea schimperi	23	P < 0.001
Euphorbia ingens	12	P < 0.05
Euphorbia tirrucalli	4	P < 0.005

Continued ...

Grewia monticola	16	P < 0.01
Grewia occidentalis	103	P < 0.001
Maytenus heterophylla	40	P < 0.001
Maytenus senegalensis	38	P < 0.001
Maytenus undata	14	P < 0.005
Olea europea africana	32	P < 0.001
Ozoroa paniculosa	37	P < 0.001
Pappea capensis	23	P < 0.005
Phyllica paniculata	9	P < 0.02
Premna mooiensis	40	P < 0.001
Ptaeroxylon obliquum	12	P < 0.001
Rhoicissus tridentata	14	P < 0.01
Rhus dentata	20	P < 0.002
Rhus pentheri	144	P < 0.001
Schotia brachypetala	23	No significance
Scolopia zeyheri	7	No significance
Sideroxylon inerme	5	P < 0.001
Tarchonanthus camphoratus	8	No significance
Vepris lanceolata	34	P < 0.001
Vitex rehmlannii	134	P < 0.001
Ziziphus mucronata	23	P < 0.002
Zanthoxylum capense	51	P < 0.001

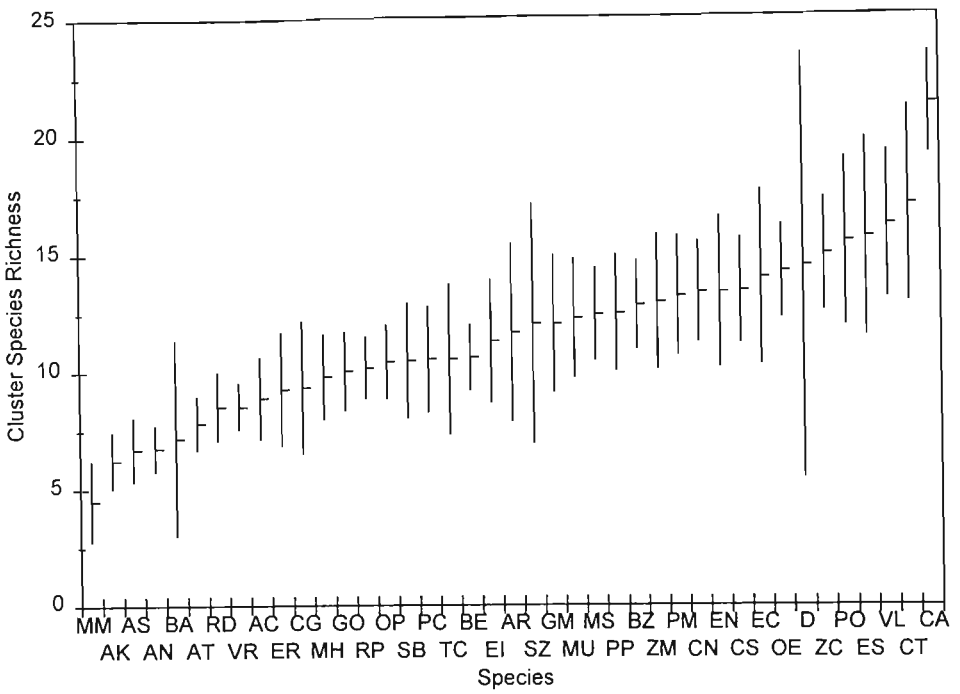

Figure 3.6. Species turn-over a 'successional' gradient (all size classes included), expressed as the 90% confidence interval on the mean species richness of clusters where each species occur. (MM - *Maytenus mossambicensis*, AK = *Acacia karroo*, AS = *Aloe spectabilis*, AN = *Acacia nilotica*, BA = *Boscia albitrunca*, AT = *Acacia tortilis*, RD = *Rhus dentata*, VR = *Vitex rehmannii*, AC = *Acacia caffra*, ER = *Ehretia rigida*, CG = *Clerodendrum glabrum*, MH = *Maytenus heterophylla*, GO = *Grewia occidentalis*, RP = *Rhus pentheri*, OP = *Ozoroa paniculosa*, SB = *Schotia brachypetala*, PC = *Pappea capensis*, TC = *Tarchonanthus camphoratus*, BE = *Brachylaena elliptica*, EI = *Euphorbia ingens*, AR = *Acacia robusta*, SZ = *Scolopia zeyheri*, GM = *Grewia monticola*, MU = *Maytenus undata*, MS = *Maytenus senegalensis*, PP = *Phylica paniculosa*, BZ = *Berchemia zeyheri*, ZM = *Ziziphus mucronata*, PM = *Premna mooiensis*, CN = *Cussonia natalensis*, EN = *Euclea natalensis*, CS = *Cussonia spicata*, EC = *Euclea racemosa zuluensis*, OE = *Olea europaea africana*, D = dead, ZC = *Zanthoxylum capense*, PO = *Ptaeroxylon obliquum*, ES = *Euclea chimperi*, VL = *Vepris lanceolata*, CT = *Cassine transvaalensis*, CA = *Celtis africana*

In conclusion;

- A `succession gradient' which is probably the result of biotic interaction among individual plants over a 'successional time scale' can explain the pattern of species distribution in a Natal bushveld community better than gradients in the physical environment.
- Species response to such a `succession gradient' can thus be used to describe the ecological function of individual species, and to group species into functional classes.
- A model describing species turn-over in bushveld communities along a continuum of `successional' development can be constructed. This model can be used to classify different communities or smaller sized units, like bushclumps, according to their successional status on the basis of their species composition. This model is a potentially useful management and planning tool.

CHAPTER FOUR: THE RESPONSE OF INDIVIDUAL SPECIES POPULATIONS TO A `SUCCESSION' GRADIENT AND THEIR CLASSIFICATION INTO FUNCTIONAL GROUPS

4.1. Introduction

The relationship describing the distribution of individuals in a population in relation to a variable, can be termed a response curve. Direct gradient analysis relates species presence (or abundance) to environmental variables on the basis of species and environmental data from the same set of sample plots (Gauch 1982). The simplest methods of direct gradient analysis involves plotting each species' abundance values against the values of an environmental variable, or drawing isopleths for each species' relative abundances in a two dimensional space representing two environmental variables. With these simple methods one can easily visualise the relationship between many species and one or two environmental variables. The significance of changes in species abundance along the gradient of a known variable can be tested using simple non-parametric statistical procedures (Zar 1974).

In the previous chapter it was shown that a gradient of cluster development status, or a `succession gradient' described by increasing cluster species richness is present in the Natal bushveld. The purpose of this chapter is to describe the species present along such a `successional gradient' and assess the significance of a successional time variable on the distribution of the individual species populations comprising a Natal bushveld community.

The response curve of each species population to this gradient can thus be used to describe the ecosystem function of each species in terms of successional time. Such description can then be used to derive a functional classification of species groups. The functional classification of species groups is a useful tool for management of vegetation (Mentis 1983). It allows one to assess the functional status of vegetation stages in plant communities that are to be managed. When this is done in relation to management objectives, it can be termed a rangeland condition assessment (Hardy & Hurt 1989, Mentis 1989). Such a system also facilitates the development of models of vegetation dynamics, so that vegetation responses to stochastic disturbance events can be predicted. Used as such, it becomes a good hypothesis generating tool for the

development of further experimental work. When conservation of species diversity, or preservation of a specific valuable species is the objective of land-use, such models are important for evaluating the status of different species populations in the landscape.

4.2 Methods

Five categories were defined by the number of woody species found in a bush cluster namely : 1-4, 5-8, 9-12, 13-16, 17-20^{+} species. These species richness categories were used to objectively define the `successional gradient' against which the occurrence of a species could be considered. The proportion of each species' population represented in each category was calculated in the following way. First, the number of individuals of a particular species were summed for each of the above categories. These numbers were then divided by the number of clusters counted in each category to give an average number of individuals per cluster (*i.e.* to normalise the data for clusters). Then the average numbers of individuals per cluster for the species were summed for the five categories and their relative abundances in each species richness category calculated. These relative abundances were then plotted against the five species richness categories to generate species response curves. To begin to separate these species into functional groups, cumulative frequency distributions were calculated for each species from early successional bush clusters with few species to later successional bush clusters with many species. The species richness category in which a species attained 40% of its cumulative frequency distribution was defined as the functional group to which that species belonged. For example, if a species attained 40% or more of its cumulative frequency distribution in the species richness category of 5-8 species, it was assigned to the early successional functional group whereas if it attained 40% or more in the 17-20^{+} it would be placed in the late successional functional group.

The classification of species into functional groups was tested statistically using a Chi-square Test for *k* Independent Samples, partitioning the degrees of freedom in the table and analysing the residuals (Siegel & Castellan 1988). The 4 X 5 contingency table, with row headings being functional successional groups 1 - 4 and column headings being the five categories of cluster species richness, was compiled using the total number of clusters in which a species was recorded as the tabulated data.

It seemed feasible to use species attributes that determine propagule dispersion and survival to explain the existence of such groups (Noble & Slatyer 1980). There is however not much known about vital attributes of all the tree species in Natal bushveld. The only species characteristic that is relatively well known for all the species is their primary seed dispersal mechanisms. Species were classified on basis of their seed dispersal strategy into three groups; (i) large herbivore dispersed, (ii) bird dispersed, and (iii) wind dispersed. Although seeds of many of the species are probably secondarily dispersed by small mammals and insects, little is known about this fourth method of dispersal for Natal bushveld species. Presumably, the scale of such secondary dispersal will be much less than the scale at which bush clusters are distributed.

4.3 Results

The species response curves for all species assigned to a functional group, using the procedure given above, were recalculated to show the relative patterns of response to the "successional" gradient (Figure 4.1). Four species, representing an average of 41.25 individuals per species, were assigned to the early successional functional group. Members of this group are encountered at least four times more frequently in the species richness category of 1-4 species than are members of the later successional groups, reach their greatest proportional representation in the 5-8 species richness category, maintain these proportions in the next two species richness categories and finally decrease to near zero in the most species-rich clusters (Figure 4.1).

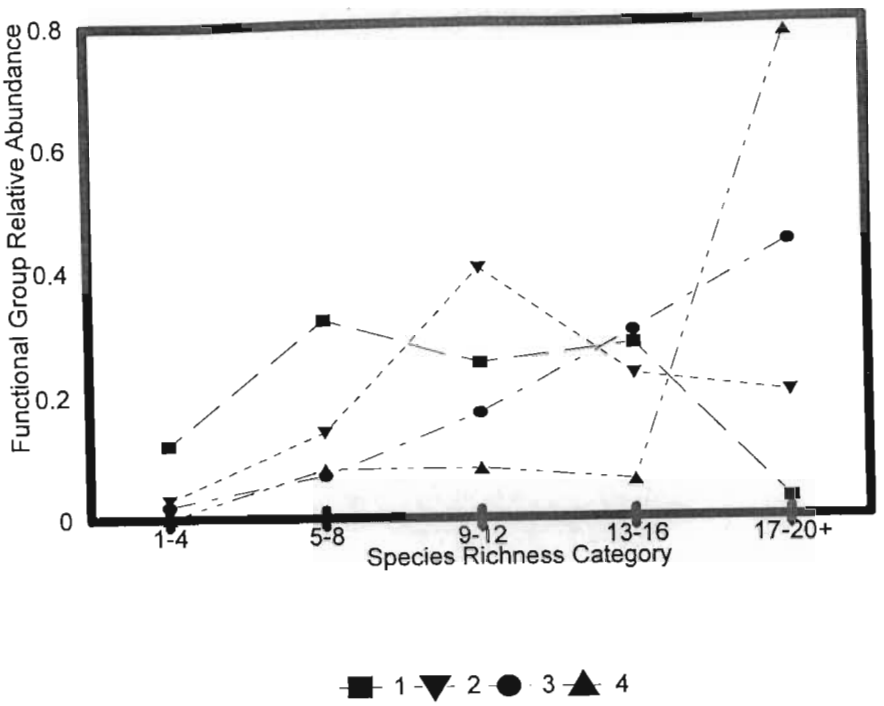

Figure 4.1. Species 'functional' group (see text) response to curves to the 'successional gradient'.

Species of the other three later successional functional groups are rarely represented in clusters comprising 1-4 species, decline in the average numbers of individuals per species and reach their highest relative abundances in the 9-12, 13-16 and 17-20^{+} species richness categories respectively (Figure 4.1). For example, members of the late successional group are never found in species clusters comprising 1-4 species, are represented by 5.33 individuals per species and reach their greatest relative abundance in the 17-20^{+} species richness category.

The individual species response curves show similar or more extreme patterns for each functional group. The early *Acacia* group is represented by roughly equal proportions in clusters with from 1-4 species through clusters with from 13-16 species after which it declines dramatically in clusters with more than 17 species (Figure 4.2a). *Aloe spectabilis*, another member of this functional group, shows a more variable pattern but is absent from the most species-rich clusters (Figure 4.2b).

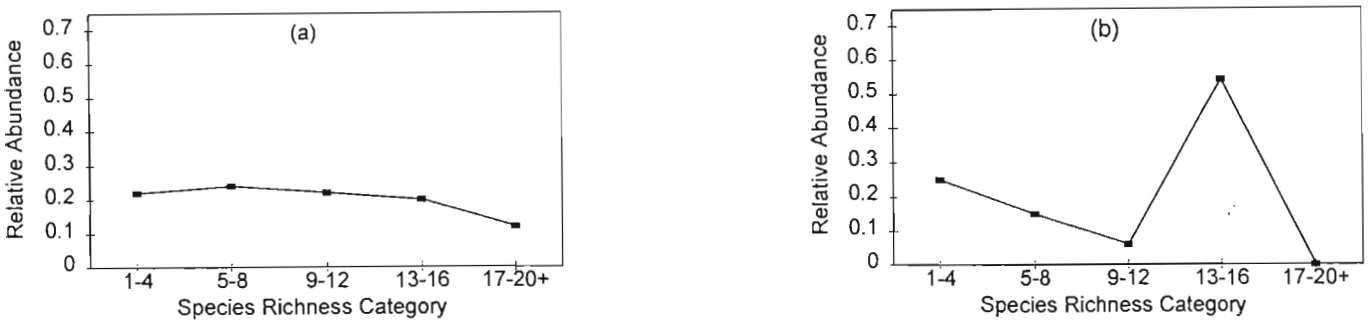

Figure 4.2 (a) Early *Acacia* group and (b) *Aloe spectabilis* response to the 'successional gradient'.

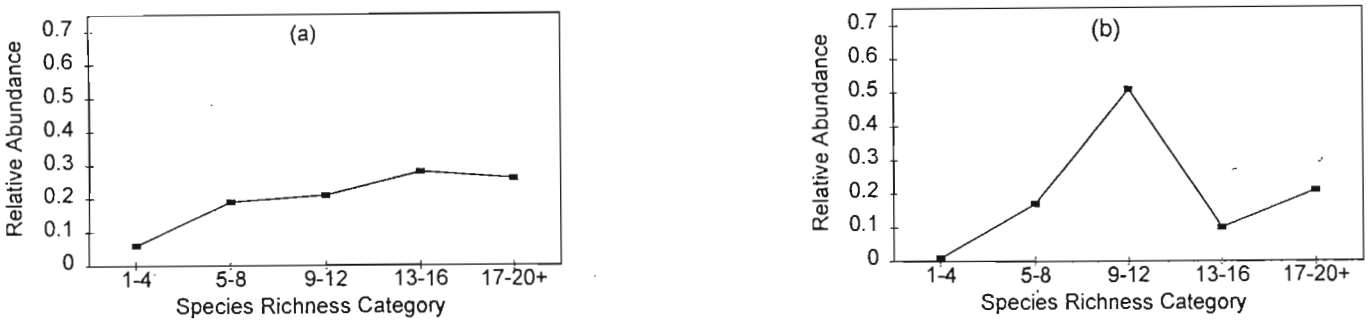

Figure 4.3 (a) *Maytenus heterophylla* and (b) *Vitex rehmannii* response to the 'successional gradient'.

Species typical of the intermediate functional groups are rarely found in the clusters with from 1-4 species (*e.g. Maytenus heterophylla, Vitex rehmannii, Euclea schimperi, Rhus pentheri, Grewia occidentalis,* and the later *Acacia* group, Figures 4.3a,b; 4.4a,b,c,d). *Maytenus heterophylla and Vitex rehmannii*, which are placed in the second category by the operational definition used above (*i.e.* clusters characterised by 9-12 species) are declining in their proportional occurrence in clusters with more than 17 species in them (Figure 4.3a,b). The later *Acacia* group, *Euclea schimperi, Rhus pentheri* and *Grewia occidentalis*, which have been placed in the third category (*i.e.* clusters characterised by 13-16 species) are more variable in their response curves with most reaching their greatest proportional occurrence in clusters characterised by the presence of more than 17 species (Figures 4.4a,b,c,d). Finally, members of the late

functional group, such as *Grewia monticola* and *Tarchonanthus camphoratus,* are only sporadically present in the first four categories and peak in clusters that are characterised by consisting of more than 17 species (Figure 4.5a,b).

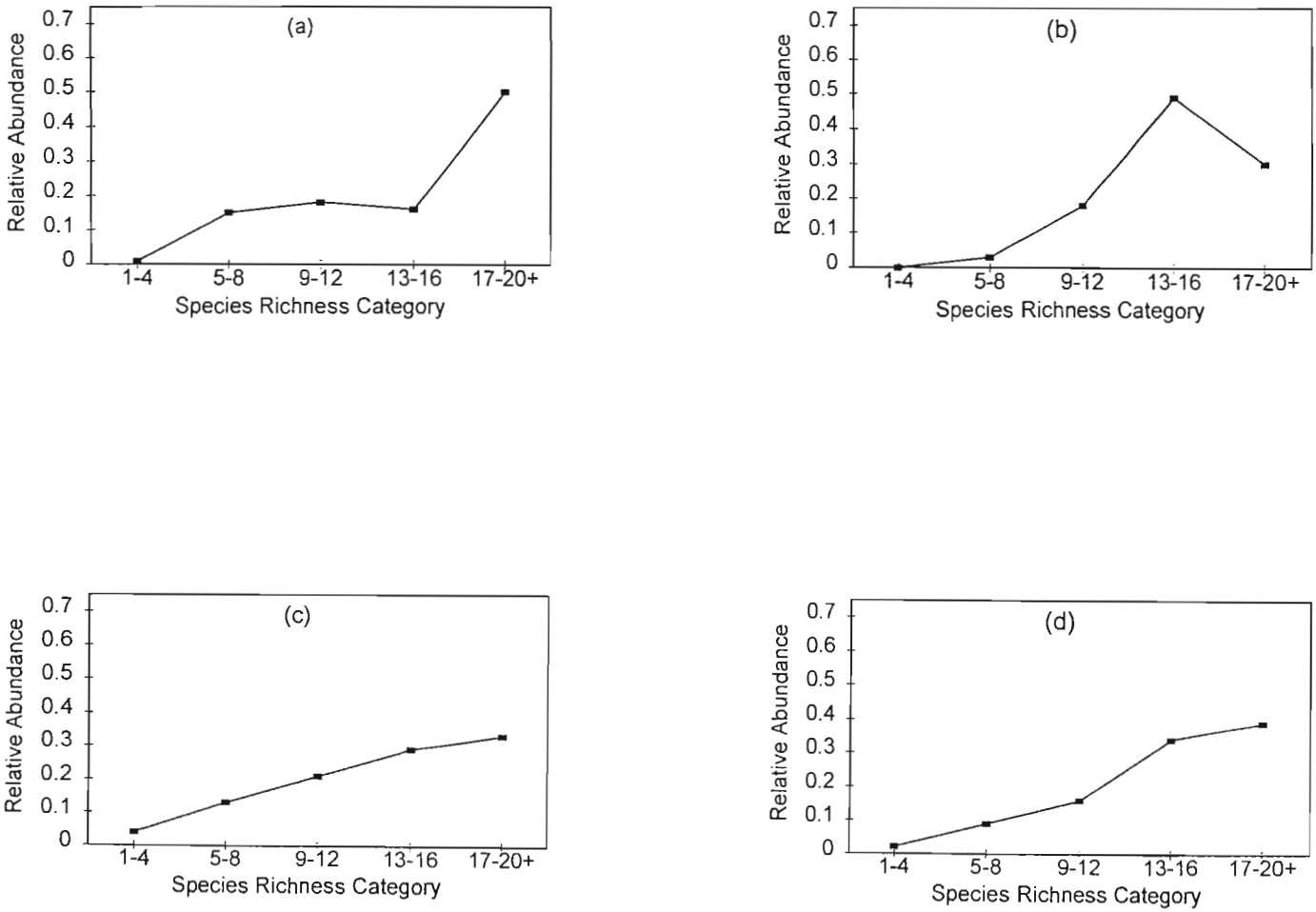

Figure 4.4 (a) Late *Acacia* group, (b) *Euclea schimperi*, (c) *Rhus pentheri* and (d) *Brachylaena elliptica* response to the 'successional gradient'.

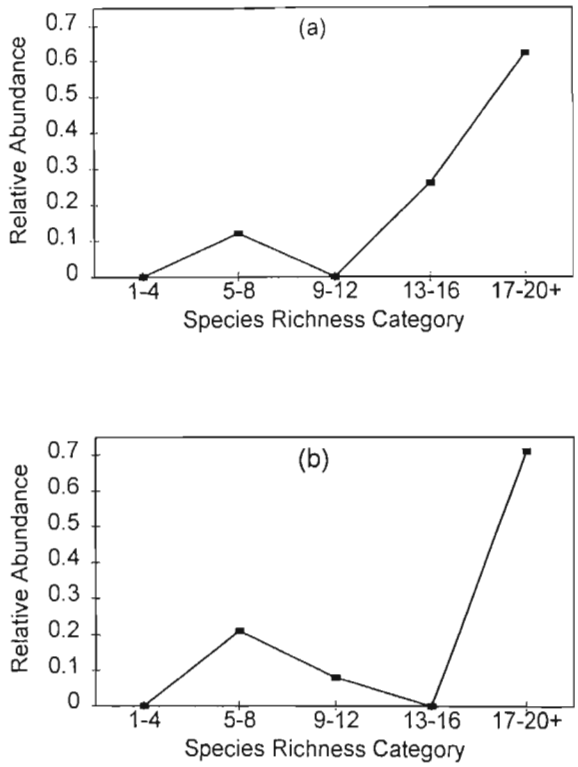

Figure 4.5 (a) *Grewia monticola* and (b) *Tarchonanthus camphoratus* response to the 'successional gradient'

To test the statistical significance of these classifications, the occurrence of each species in a bush cluster, characterised by its species richness category was compared with the expected number (Table 4.1). Analysis of the residuals indicated that significant differences were occurring in the groupings of species into functional groups (Table 4.2). In the species richness category of one to four species, for example, the early successional functional species occurred significantly more often than expected ($P < 0.01$) while the late successional functional species occurred significantly less often than expected ($P < 0.01$). No significant differences were present in this species richness category for the intermediate functional groups. In contrast, in the comparison of observed and expected occurrences for bush clusters comprised of 17 or more species, the early successional functional species were observed less often than expected ($P < 0.01$) while the late successional functional species were observed more frequently than expected ($P < 0.01$).

Table 4.2 can also be read across the columns. For example, members of the early successional functional species group occurred significantly more often than expected in bush clusters characterised by one to four and five to eight species and then switched such that the observed number of occurrences in bush clusters comprised of nine or more species occurred less often but not always significantly so (Table 4.2). The opposite pattern is found in the late successional functional species group. The intermediate functional species groups are not as clear. Functional species group 2 had significantly more occurrences than expected in the species richness category of 9-12 species ($P < 0.01$) with no other species richness categories being significant for this group (Table 4.2). Functional species group 3 had significantly more occurrences than expected in species richness category of five to eight species ($P < 0.01$) and significantly fewer occurrences than expected in the species richness category of 17-20^{+} species ($P < 0.01$) while no significant differences occurred for these two intermediate functional groups in the other species richness categories (Table 4.2).

The primary dispersal modes for members of each functional group tend to vary within and between groups (Table 4.3). Within groups, all dispersal modes are found but their proportional occurrence changes between groups. For example, in the early successional group (Group 1) 100% of the species are potentially dispersed by large herbivorous vertebrates. The seeds of the fourth species in this group, *Aloe spectabilis*, are primarily wind-dispersed with secondary dispersal by small rodents.

Table 4.1. The observed and expected numbers of occurences in bush clusters for members of each functional species group in a species richness category.

	Upper Limit of Species Richness Category				
	4	8	12	16	20+
Observed					
Group 1	144	148	59	58	18
Group 2	21	55	62	33	48
Group 3	27	93	50	51	27

Continued ...

Group 4	55	205	164	173	364
Expected					
Group 1	56.9	115.3	77.1	72.5	105.2
Group 2	29.2	59.1	39.5	37.2	53.6
Group 3	33.0	67.0	44.8	42.1	61.1
Group 4	128.0	259.5	173.5	163.2	236.7

Table 4.2. The probabilities and directions of differences based on partitioning the degrees of freedom and analysing the residuals for the 4 x 5 contingency table for functional species groups and species richness categories. + = observed > expected, - + observed < expected

	Upper Limit of Species Richness Category				
	4	8	12	16	20+
Group 1	P< 0.01+	P< 0.01+	P< 0.05-	N.S. -	P< 0.01-
Group 2	N.S. -	N.S. -	P< 0.01+	N.S. -	N.S. -
Group 3	N.S. -	P< 0.01+	N.S. +	N.S. +	P< 0.01-
Group 4	P< 0.01-	P< 0.01-	N.S. -	N.S. -	P< 0.01+

Table 4.3 The primary dispersal mode of tree species assigned to the four functional groups based on their occurrence in species richness categories. Group 1 = early successional species, Groups 2, 3 = intermediate successional species, Group 4 - later successional species. Modes of dispersal are; I = large hervivorous vertebrates, II = birds, III = wind. ? = possible dispersal mechanism

Mode of Dispersal	I	II	III
Group 1			
Acacia karroo	X		
Acacia nilotica	X		

Continued ...

Acacia tortilis	X		
Aloe spectabilis			X
Group 2			
Calpurnia aurea	X		
Euclea natalensis	?	X	
Maytenus heterophylla	X	X	
Rhus tomentosa	X	X	
Vitex rehmannii	?	X	
Group 3			
Acacia ataxacantha			X
Acacia caffra			X
Acacia robusta			X
Berchemia zeyheri		X	
Brachylaena elliptica			X
Cussonia spicata		X	
Ehretia rigida		X	
Euclea racemosa		X	
Euclea schimperi		X	
Grewia occidentalis		X	
Maytenus senegalensis		X	
Olea europaea		X	
Ozoroa paniculosa		X	
Pappea capensis	X	X	
Premna mooiensis		X	
Rhus pentheri		X	
Schotia brachypetala	?	X	
Zanthoxylum capense	X	X	
Ziziphus mucronata		X	

Continued ...

Group 4			
Celtis africana	X	X	
Cussonia natalensis		X	
Grewia monticola		X	
Rhus dentata	?	X	
Sideroxylon inerme	X	X	
Tarchonanthus camphoratus			X

This species is not a member of the guild of bush cluster species as it is found in open savannas growing by itself. Its presence in the bushclusters is a result of the overgrowth of early successional species such as *Acacia nilotica* and *A. tortilis*. Four of the five members of the first intermediate successional group (Group 2) have a mixed primary dispersal strategy with their seeds being moved either by large herbivores or by birds. In contrast, 65% of the species in the later intermediate successional group (Group 3) and over 83% in the late successional group (Group 4) have seeds that are primarily bird-dispersed. Many members of the latter two groups also have their seeds dispersed by monkeys.

4.4 Discussion

There appear to be four distinct patterns of distribution or species response curves as the species richness of the bush clusters increases; an early successional guild, a late successional guild and two intermediate successional guilds, one which is specialised and the other which consists of more generalist species. It must be kept in mind that these patterns reflect characteristics of groups of species and not individual species. For most species these response curves are based on small data sets. Hence, these results should be used chiefly to generate hypotheses on the `successional status' of the different species. In order to model response of any individual species to the `succession' gradient larger data sets on the relationship of individual species' occurrence and cluster (community) species richness, subject to more environmental variation, should be obtained. As the objective of this specific project is to generate a

model that can be used as a hypothesis for future research, detailed studies of individual species population response to a `succession' gradient falls outside the scope of the project. Thus `successional' or functional status of any species must be viewed as relative, not only to species in another group, but to the species within the group as well. As a result, there exists a hierarchy of `successional' status between and within groups. However, no attempt has been made to order species according to such a hierarchy within groups.

Despite the above, some species response curves can be explained simply as the result of differential dispersal mechanisms. For example, all members of Functional Group 1 are dispersed by large herbivorous vertebrates. *Aloe spectabilis*, as mentioned previously is sporodically present in grasslands and is incorporated into the bush clusters as they form and expand in size. This species does not initiate the formation of a bush cluster. The remaining species in this group are members of the genus *Acacia*. These `pioneer'"species are common outside clusters or as mono-specific stands on recently disturbed areas such as abandoned fields (Edwards 1967). They are also the species most commonly cited as being involved in the encroachment of bush into grasslands in KwaZulu-Natal during the last one hundred years (Bews 1917, West 1951, Comins 1953, Edwards 1967, Wells 1967, Moll 1976). All of the three species of *Acacia* in this group are dispersed by large herbivores (Palmer & Pitman 1972, Van Wyk 1972, Coe & Coe 1987; Hurt & Yeaton 1992, 1993; J. E. Granger, **personal communication**).

The seeds of members of Functional Group 2 tend to be either moved by large herbivores or by birds or by both modes of dispersal (Palmer & Pitman 1972, Coates Palgrave 1983). As a result these species are common outside bush clusters, are found in a wide range of clusters but tend to be most common in bush clusters of intermediate species richness. The vegetation dominated by these species is characteristic of the earlier stages of the cluster phase development of Natal bushveld. Often vegetation is maintained in this state by recurrent disturbance events, such as fire and drought. Where these species occur as large individuals outside bush clusters, a situation in which the cluster phase process has been reversed by some extreme disturbance event is indicated. Such an event can be a fire, a drought, exploitation of wood resources by people, or a combination of these of these factors.

In contrast, members of Functional Group 3 are more generalised in their species response curves occurring more frequently than expected (although not significantly so) in all categories of bush cluster species richness except for the lowest and the highest ends of this scale. Most of these species have seeds which are bird-dispersed. An exception to this dispersal mode are the members of a later successional series of *Acacia* species which have dehiscent pods and release their seed while the pods are still on the tree. Seeds of this group may be primarily dispersed by wind and secondarily by small rodents
(Hurt & Yeaton 1992, 1993). This functional group is represented by a wide range of species that are characteristic of closed-canopy savanna woodlands but which may occur seldomly in forest communities or be subdominant members of the forest communities. Species, that are characteristic of closed canopy woodland, are usually associated with ecotones or canopy gaps when they occur in forests (Edwards 1967, Moll 1976, 1985, Coates Palgrave 1983, Acocks 1988). Members of this functional group are probably opportunists that survive in the landscape because of frequent disturbances but which depend on the later cluster phases of the Natal bushveld for germination and survival of the smaller size classes. In contrast, other members of this functional group may be subdominant within the forest and have very specific microsite requirements for germination and establishment. They only rarely become members of the upper canopy stratum but potentially can become large trees (Coates Palgrave 1983, Moll 1985). Many of these species are also commonly associated with semi-deciduous forest communities on rocky outcrops and stream banks (Killick 1959, Edwards 1967, Moll 1976, Coates Palgrave 1983, Acocks 1988). Little is known about the natural requirments for `safe' microsites for members of this functional group.

Members of the late successional functional group represent species that occur at the end of the succession development spectrum in forest. In South Africa a forest is defined as a community of woody plants with a closed canopy between 10 m and 20 m in height, with usually a poorly developed herbaceous layer and which are little affected by veld fires (Acocks 1988). Species response curves are poorly represented for members of this functional group as the numbers of individuals censused to delineate them are small. Most of the species in this group are common in coastal and mist-belt forests in KwaZulu-Natal (Acocks 1988). In Clementsian terminology these

can be termed `climax species' (Clements 1916). Vegetation dominated by these species has probably either developed beyond the discrete bush cluster phase of the Natal bushveld, or characterises a very advanced state of cluster development. It is interesting to note that where this advanced state has been severely disturbed, these semi-deciduous broadleaved `forests' are being replaced by succulent forest (Killick 1958, Wells 1959, Morris 1967).

Species, the seeds of which are dispersed by large herbivores, are limited to Functional Groups 1 and 2. It is known that intense predation of *Acacia* seeds by many species of bruchid beetles (Bruchidae) does occur (*e.g.* Coe & Coe 1987). A seed dispersal mechanism, that ensures the transport of seed away from parent trees, is a sound strategy for tree species that suffer intense seed predation. Seed dispersal by large herbivores offers such a mechanism. Large herbivores are generally not limited to a narrow range of vegetation structure as occurs with birds and small mammals. They readily feed in woodland and in grassland, thus transporting plant propagules from the one structural vegetation phase to another.

In southern Texas, *Prosopis glandulosa*, a leguminous tree which plays an analogous role to the three *Acacia* species of Functional Group 1, and its associated bush clusters were restricted to drainage lines when the first European settlers arrived. Unlike the situation in Natal bushveld, most of the North American large herbivore fauna became extinct at the end of the Pleistocene (Martin & Klein 1984, Janzen 1986). Within a century after the large-scale introduction of cattle, these woodlands started to spread into grassland areas (Archer 1989, 1990). Now, `bush encroachment' is a serious challenge to cattle ranching in Texas and Arizona (Glendenning 1952). Brown and Archer (1987) showed that in Texas, seeds of *Prosopis glandulosa* have increased germination, establishment and survival potential when they are deposited in cattle dung. This is probably the result of (i) the effects that mastication and the digestive process might have on breaking dormancy, (ii) a nutrient-rich establishment site provided by the breakdown of the dung and (iii) the effect the dung has on suppressing grass cover. It is also known that areas that are intensively used by cattle are more prone to the establishment of these `pioneer woody' plants than areas that have been less intensively utilised, or where cattle have been excluded (Brown & Archer 1989; Skarpe 1990a,b; **personal observation**).

`Bush encroachment' also coincides with intensification of the cattle industry in southern Africa and in particular, in Natal bushveld. It is difficult to determine whether `bush encroachment' was caused by the intensification of the cattle industry or by other factors. It is probable that the practice of moving cattle from `winter grazing' in the bushveld areas to `summer grazing' in the higher altitude grassland areas, the simulataneous replacement of a diverse large mammal fauna with a single species system, and forced intensive grazing systems using paddocks or concentrating large numbers of subsistence farmers in relatively small areas have been important causal factors of `bush encroachment'. These factors would have influenced vegetation dynamics by (i) moving *Acacia* seed from bushveld areas to grassland areas, (ii) reducing the impact of browsing animals on the establishment and survival of trees, (iii) reducing the herbaceous biomass and thus reducing fuel loads and the impact of fire on the survival of trees, and (iv) creating local arid conditions through exposure of bare soil and lowering of the water table.

In addition to the above, many marginal areas of Natal bushveld had in the past been ploughed for maize production and subsequently abandoned. It is these old-fields that are most prone to invasion by *Acacia* species. Also, in some areas intensive, broad-scale, use has been made of insecticides to control insect `pests' such as tsetse fly and grasshoppers. Such use of herbicides could have created a mass seeding event of *Acacia* species by reducing seed predation by insects.

All species belonging to the later successional groups (Groups 3 and 4) have seeds which are either bird or wind dispersed. Nearly all these species occur almost exclusively inside bush clusters. Bush clusters act as a buffer against a variable physical environment and inhibit the growth of grasses beneath them. Seeds that are deposited in the open do not have any buffer against environmental variation and the chances of successful germination and seedling survival are probably reduced because of this factor and because of intense competition from grasses.

Most of the Functional Group 3 and 4 species that seem to be dependant on the late successional bush cluster or woodland phase need a seed dispersal strategy that allows the maximum number of seeds to be deposited in favourable growing sites, away from the parent plant. Seeds from fruits eaten by birds are deposited where birds defecate. This depends on where birds forage, rest, nest, perch or seek refuge from

predators. Two types of seed dispersal patterns are found with frugivorous birds. They are (i) `specialised' dispersal, in which a small number of dispersers deposit the seeds in high quality sites and (ii) `risk-spreading` dispersal, where many seeds are carried by many dispersers and deposited in a large number of habitat types (Izhaki *et al* 1991). Fuentes *et al* (1984) reported that seed rain was important only around bird perches in bush clusters in Chilean matorral . Nursing by shrubs, and not by rocks or fallen branches, was a requirement for the survival of matorral shrub seedlings. Also seedlings in bush clusters were more protected from herbivory and desiccation than seedlings in the open. Finally, there were fewer seeds deposited between bush clusters in the Chilean study.

Similarly, it has been suggested that birds depositing seeds in their faeces when they perch, are responsible for the clustered structure of bushveld in South Africa. In the xeric succulent thicket of the Eastern Cape, seed that is deposited beneath the canopies of individuals of *Acacia karroo* has a higher germination and survival rate than seed deposited in the open, or beneath the canopies of a broadleaved shrub, *Rhus undulata* (Briers & La Cock 1991). La Cock (1992) found that in `mature' xeric succulent thicket of the eastern Cape, seedlings survived only inside bush clusters, and that *Pappea capensis* was the most prominent nurse plant.

The distribution and movement of frugivorous birds is obviously determined by the availability of fruiting plants and a vegetation structure that offers sufficient cover and perches. In savannas, these birds will most likely be associated with the closed woodland and coalescing cluster phases and to a lesser extent with the open savanna phase. They would be rare in the grassland phase. Plant species that rely on birds to disperse seeds will only be able to expand their range in any landscape once sufficient structure has been created by the `pioneer' woody plants to attract birds from the woodland or cluster phase. Obviously, as a woody vegetation community becomes more species rich and increases in area it will attract a larger number and variety of birds and, in turn, accelerate the deposition of seed.

In the Chillean mattoral the presence of seed and seedlings of wind dispersed species is concentrated in bush clusters, probably because of interception of seed or reduced wind speed in bush clusters (Fuentes *et al* 1984). A similar pattern is to be found in arid parts of Australia (Eldridge *et al* 1991) and in semi-deciduous tropical

forests in Kenya (Kigomo *et al* 1990). For woody plants, at least, successful dispersion of seed by wind seems to positively related to density of woody canopy cover. It can thus be expected that woody plant species with wind-dispersed seeds will be largely limited to the closed canopy woodland and cluster phases of savanna landscapes. `Bush encroachment' by herbivore dispersed `pioneer' trees and shrubs into open areas is thus a prerequisite for the slow range expansion of wind-dispersed species.

Invasion of grasslands by `pioneer' woody plants is likely to be an event driven process. Events that increase (i) the amount of viable seed that is produced, (ii) the dispersal of viable seed into grasslands, (iii) the germination of seed, or (iv) the survival of seedlings, should lead to increased establishment of these trees. This process should be rapid. In contrast, establishment of woody plants with bird- or wind-dispersed seed is likely a slow process of diffusion. The rate of this process is determined by the rate of invasion of grasslands by `pioneer' species and the development of vegetation structure that will attract frugivorous birds, and the distance from `later successional' communities. A similar pattern is evident in the Chillean mattoral (Fuentes *et al* 1986) and in the mesquite woodlands of Texas (Archer *et al* 1988).

When viewed in long-term time scales, it would seem that pulses of `bush encroachment' and subsequent break-up of the closed canopy woodland and bush cluster phases of savanna landscapes are responsible for the maintenance of woody species richness in the Natal bushveld. It therefore seems possible to classify savanna landscapes in KwaZulu-Natal into two broad categories; (i) old bushveld, characterised by a well-developed, closed-canopy woodland and a mosaic of bush cluster phases differing in species richness and (ii) young bushveld, characterised by the dominance of the open grassland and open savanna phases, or mono-specific thickets of `pioneer' species. I suggest that succession of woody vegetation in young bushveld is deterministic and driven by facilitation. This succession might be arrested by recurrent disturbances such as fire and drought, and competition between seedlings of `pioneer' woody plants and grass. In old bushveld, succession is cyclical and is driven by competition. In old bushveld, well-developed bush clusters provide a buffer against the effects of recurrent disturbances such as fire and drought, and these disturbances act mainly to keep local-scale successional processes such as the formation of new bushclumps and the expansion of old bush clusters under control. For example, large

individuals (stem diameter exceeding 50 cm) of relatively slow growing species, like *Olea europaea* that were recorded in large clusters, suggests that some of these clusters are very old and emphasises the role of bush clusters in stabilising a variable environment at the local (micro-) scale.

CHAPTER FIVE: TEMPORAL GROWTH AND STABILITY OF WOODY PLANT CLUSTERS IN THE WEENEN DISTRICT

5.1. Introduction

Archer *et al.* (1988) analysed aerial photographs as a direct assessment of changes in savanna/woodland composition in southern Texas. They found that changes in this system were closely related to rainfall. Total woody plant cover increased during the period 1941-1983. Mortality of small clusters occurred in periods of dry years. However, in periods of average or above average rainfall, the appearance of new clusters would off-set these losses. Cluster expansion was a dynamic process and, over the period of study (1941-1983), showed an overall increase in size.

As many of the inferences about Natal bushveld made in the previous chapters have shown a strong similarity to the situation reported by Archer and his co-workers (Archer *et al* 1988), the objectives of this chapter were to analyze a sequence of three sets of aerial photographs taken in 1940, 1964 and 1985, covering a 45-year period, to :

i) see if the changes in woody plant cover, and hence the pattern of woodland succession, are related to wet and dry periods,

and

ii) measure the spatial growth of individual bush clusters in order to determine the direction and the rate of opening or closure in the savanna/woodland mosaic.

5.2. Methods

Aerial photographs, at an approximate scale 1 : 10 000 of the `Darkest Africa' and Weenen study sites, taken in 1940, 1964 and 1985, were obtained from the South African Department of Land and Regional Affairs. Because of distortion inherent in aerial photographs, and scale differences between the 1940, 1964 and 1985 photos, a mean scale was calculated for each of the set of photographs. Scales were corrected by comparison with the relevant South African Director-General of Survey 1 : 50 000 topo-cadastral maps. The scales, compared to three known distances on the 1 : 50 000 map, were calculated for each set of aerial photographs. The mean of these three scales for each set of aerial photographs was then used for this analysis. As only

relatively short distances were to be measured from these aerial photographs, the variation on the mean scale of the photo should not have a significant influence on measurements made.

A line-intercept measurement (Phillips 1959) was used to determine the proportion of woody cover. Three sites that could be accurately identified on the 1940, 1964, and 1985 photos were used, two sites at the `Darkest Africa` study site and one at the Weenen study site. A grid, 1000 m long by 500 m wide and divided in fifty 100m by 100m quadrats (1 hectare), was drawn to scale for each of the three sets of photographs. These grids were photocopied onto clear acetate sheets and then placed over the respective aerial photograph for each site. The sites were then viewed through a eight-times magnification dissection microscope and the intercept with woody canopies along ten 500 m long transects measured to the closest 0.25 mm, using a ruler. All canopy intercepts smaller than 0.25 mm (= 2.5 m) were recorded as point measurements. For analysis all measurements were converted to meters. All point values were given an arbitrary value of one meter. For each site the woody canopy intercepts along the set of transects were summed. Woody cover was expressed as the proportion of total canopy intercept per 100 m of transect length. This procedure was repeated for each of the three sets of aerial photographs.

Identification of individual bush clusters on aerial photographs taken at the three intervals was extremely difficult. Twenty-five clusters could be identified consistently on all three aerial photographs for the `Darkest Africa' study site. At the other two study sites, where intense resource exploitation took place, vegetation changes appeared to be changing too rapidly to identify individual clusters on all three sets of photographs. Only large clusters (< 30 m^2) could be individually identified on all three sets of aerial photographs. Small clusters and individual trees either disappeared during the intervals between the taking of the aerial photographs or coalested with adjacent clusters. The 25 clusters on the Darkest Africa site were viewed through a stereoscope at eight-times magnification. Two perpendicular axes were measured for each cluster using a stereometer bar. This procedure was repeated for each of the three sets of aerial photographs. An index of cluster area was then calculated as the area of circle of which the radius is the mean of the two perpendicular cluster axes. ANOVA was used to test the significance of changes in cluster area between 1940, 1964 and 1985.

5.3. Results

A significant change in the proportion of woody plant cover occurred for the combined measurements made on the aerial photographs at `Darkest Africa' and Weenen sites during the period 1940-1985 (Table 5.1, $F_{2,87} = 6.3$, $P < 0.05$). No significant difference was observed between the proportion of woody plant cover for the years 1940 and 1985 but 1964, at the end of the drought period, was 27% lower in woody plant cover than the other two time intervals measured (Tukey multiple range test, $P < 0.05$). For the two sites measured at `Darkest Africa', the relatively undisturbed site, the year 1985 had at least a 27% higher woody plant cover than in the 1940 and 1964 (Table 5.1, $F_{2,57} = 9.2$, $P < 0.001$, Tukey multiple range test, $P < 0.05$) whereas at Weenen, the labour farm with intensive subsistence farming during the 1940's and later, woody shrub cover decreased significantly by 57% from 1940 to 1964 and had not yet recovered to its 1940 cover by 1985 (Table 5.1, $F_{2,27} = 25.2$, Tukey multiple range test, $P < 0.05$) despite management efforts by the Department of Agriculture and the Natal Parks Board.

Table 5.1. The mean and standard error X ± S.E.) per 100 m of line transect for the proportion of woody plant cover at two sites at 'Darkest Africa' and one site at Weenen measured from aerial photographs for the years 1940, 1964 and 1985. n = number of line transects measured.

Site	n	1940	1964	1985
'Darkest Africa'	20	0.15 ± 0.01	0.14 ± 0.01	0.19 ± 0.01
Weenen	10	0.14 ± 0.01	0.06 ± 0.01	0.08 ± 0.01
All Sites	30	0.15 ± 0.01	0.11 ± 0.01	0.15 ± 0.01

Mean cluster size at `Darkest Africa' increased nearly two-fold from 1940 to 1964 and 1985 but showed no significant change from 1964 to 1985 (Table 5.2, $F_{2,71} = 4.7$, $P < 0.02$, Tukey multiple range test, $P < 0.05$).

Finally, comparing these data for the growth rates of different sized bush clusters over the 45-year period, small bush clusters (<100 m^2) showed a 62% increase in size from 1940 to 1964 but decreased by 10% from 1964 to 1985. Intermediate-sized bush

clusters (100-400 m^2) increased by 54% during the 1940-1964 period but decreased by 29% during the period 1964-1985. Only large bush clusters (>400 m^2) maintained stable rates of growth increasing by 7% from 1940 to 1964 and 8% from 1964 to 1985.

Table 5.2. The mean size and standard error (m^2) for twenty-five bush clumps measured at 'Darkest Africa' over the period 1940-1985.

Year	X ± S.E.
1940	62.5 ± 11.5
1964	142.9 ± 23.0
1985	108.0 ± 17.5

5.4. Discussion

Archer (1990) described fluctuations in woody plant cover in the savannas of southeastern Texas from aerial photographs covering the same period as those of this study for the Natal bushveld. These fluctuations were, in both cases, due to severe drought conditions experienced during the 1950's followed by a sequence of above-average rainfall during the 1970's. In the Natal bushveld, the period from 1940 to 1964, and especially the last 13 years (1951 to 1964) experienced a markedly below average rainfall (nine out of 13 years were below average during this period, see Figure 1.2). In contrast, the period 1964 to 1983, especially the last 10 years (1971 to 1983) experienced above average rainfall (nine out of twelve years were above average during this period). However, the magnitude of these fluctuations varied between the two continents. In Texas, where total woody plant cover on the study site increased from 13% in 1941 to 36% in 1983, there was only a slight decrease during the drought years (1941-1960) followed by a three-to-eight-fold increase during the wet period (1960-1983). In contrast, the magnitude of the Natal bushveld changes were much greater during the drought years and varied between sites depending upon their landuse history. The relatively undisturbed `Darkest Africa' site decreased only 7% from 15% woody plant cover to 14%. However the Weenen site, which was a labour farm during at least the early part of the drought period and was undergoing a process

of veld rehabilitation, which included some bushcutting, during the wetter period, showed a 57% decrease in woody plant cover from 14% in 1940 to 6% in 1964. In addition, recovery from the drought period also varied according to landuse practices. At `Darkest Africa' the woody plant cover increased to 19%, a gain of 36% from 1964 while at Weenen, woody plant cover increased to 8%, a gain of 33% from the end of the drought period. While the per cent gains are roughly equivalent for the wetter years at both sites, the Weenen site, with its history of heavy landuse in the past, showed an overall loss of woody plant cover during the 1940-1985 period represented by the aerial photographs. In contrast, there was an overall increase in total plant cover of 27% for the relatively undisturbed `Darkest Africa' site during the same period.

Archer (1990) reported also that increases in total woody plant cover were the combined results of cluster enlargement in the uplands and upslope migration of closed-canopy woodlands. In the Natal bushveld study closed-canopy woodland margins were not considered due to their absence in the region studied which, in part, appears to be due the large differences in topography occurring between the Texas and KwaZulu-Natal study sites. Drainage lines in the steeply-sloping topography of the Natal bushveld are relatively drier over the course of a year than are those that would occur in a more gradually sloping region such as that of the La Copita study site in southeastern Texas. As a result, closed-canopy woodland in the upland regions of KwaZulu-Natal does not develop to the extant that such vegetation would in southeastern Texas.

However, there does appear to be extensive enlargement and coalescence of bush clusters in KwaZulu-Natal. There was a two-fold increase in the average size of bushclusters during the drought years, which declined only slightly during the wetter period. The latter decline may have been due to loss of *Acacia* spp. from the canopy of the bush cluster as a result of successional replacement by broad-leafed tree species during the 45-year period covered by the sequence of aerial photographs. It may also be due to increased mortality of a species such as *A. karroo*, which colonises the margins of these bush clumps. This species would be susceptible to hot fires which would occur in the dry season of the wetter years due to the increased fuel load of the herbaceous layer. Furthermore, the difficulty of identifying bush clusters consistantly from aerial photograph to aerial photograph is due to coalescence of adjacent bush

clusters. Since only bush clusters which could be identified from one set of aerial photographs to another were measured, the results reported for Natal bushveld suggest that overall rates of bush cluster growth may be underestimated for this vegetation and this region.

The results from the `Darkest Africa' site in the Natal bushveld show that, while average bush cluster size has doubled during the drought years, overall woody plant cover declined. Thus, it seems reasonable to argue that the effect of prolonged droughts or severe drought events kills individual plants in this vegetation type. Also, it is logical to argue that there is increased establishment, survival and growth of woody plants during periods of above-average rainfall or following events of above-average rainfall. `Bush encroachment' thus seems to be a cyclical, event-driven phenomenon in which woody plant cover increases during wet periods and decreases during dry ones. However, the overall trend in succession for Natal bushveld, as it is in the savannas of southeastern Texas (Archer 1990), is towards closed-canopy woodland if the processes functioning during the 1940-1985 continue and no density-dependent factors or changes in landuse practices or management occur. Such cycles of `bush encroachment' are thus important for the initiation of new bush clusters and for the maintenance and growth of older bush clusters. As a consequence, these cycles are important in the maintenance of bio-diversity in Natal bushveld. Firstly, they act as a source of disturbance which leads to patterns of different ages and sizes of bush clusters across the landscape. Secondly, because the effects of climatic perturbations are more severe on the `open savanna' phase of the Natal bushveld than on the cluster phase, woody bush clusters act as a buffer against variation in climate which affects moisture availability to plants. Thus, it is no wonder that most of the woody species in the Natal bushveld only occur in the bush cluster phase or in closed-canopy woodlands along drainage lines. When the ripple effect of other organisms that are dependant on these species is included, the importance of the cluster phase of the Natal bushveld for the maintenance of bio-diversity and ecosystem resilience is greatly accentuated.

CHAPTER SIX: GENERAL DISCUSSION

It is becoming increasingly evident that species distribution and community structure on `natural' landscapes are not directly related to the physical-chemical nature of the habitat. The effects of plant growth on altering physical-chemical properties of the habitat at the local scale usually mask the `inherent' habitat characteristics. Woody plants tend to have a long-term effect on their habitat because they are generally long-lived which results in `ecosystem hysteresis' or `ecosystem memory' (Van Hulst 1980). In arid and semi-arid areas the development and dynamics of vegetation seem to be determined by stochastic disturbances that retard linear succession resulting in complex combinations of cyclical successions (Yeaton 1978, 1988) or replacement sequences (Yeaton & Manzanares 1986). Species' vital attributes that determine the success of propagule dispersal or survival following disturbance events (Noble & Slatyer 1980) and a species' potential to respond to rainfall and increased soil moisture levels (Westoby 1979) are important determinants of vegetation development and dynamics in arid and semi-arid regions. The Natal bushveld landscape can be classified as a semi-arid savanna because its rainfall is spatially variable and unpredictable even though it falls seasonally and its long-term annual mean exceeds 600 mm in many places (Chapter 1). As a consequence, most of the plant life-forms in Natal bushveld are adapted to periodic limiting moisture availability. It is thus hardly surprising that the effects of `primary' determinants, such as rainfall and soil nutrient status (Walker 1985, Teague & Smit 1992), and `secondary' determinants, such as fire, herbivory and human activities, on species distribution and community structure in savanna landscapes are often difficult to distinguish between (Ben-Shahar 1990, Nott 1991).

The traditional range succession model based on convergent succession to a `climax' condition, and various `sub-climax' or seral conditions (Clements 1916, Tansley 1935, Phillips 1935, Weaver & Clements 1938) does not seem to explain all the observed variation of community structure in arid and semi-arid environments (Gleason 1926, Drury & Nisbet 1973, Connell & Slatyer 1977, Westoby 1979). For use as a range management and classification tool (Dyksterhuis 1949, Foran 1973, Tainton 1981, Acocks 1988) this traditional range succession model is probably inadequate for use in the southern African savannas (Goodman 1991, Mentis *et al* 1989).

Opportunistic management of savanna rangelands, based on `state and transition' models (Westoby *et al* 1989) are probably more appropriate. According to these models various `states' of vegetation structure can exist in a specific rangeland. These states are generally not at equilibrium and `transitions' from one state to another may occur over time. Such `transitions' can be caused by catastrophic disturbance events, autogenic succession (Archer *et al* 1988) and cyclical succession (Yeaton 1978, 1988; Yeaton & Manzanares 1986).

Natal bushveld can be described as a savanna with four structural vegetation phases that occur across the landscape. These phases are open grassland, open savanna (where single trees occur in a grassland matrix), bush clusters (where discrete bush clusters occur in a matrix of grassland or open savanna) and a closed-canopy woodland. These vegetation phases can be used as states in the development of a simplified state and transition model. The model can be made more complex by subdividing the bush cluster phase into pioneer, mature and coalesced bush clusters and by recognising additional states, such as woodland margins (Scanlan & Archer 1991). This thesis deals specifically with the dynamics of the bush cluster phase but attempts to determine, to some extent, the direction and rate of transition to other states.

Bush clusters affect the micro-climate and soil characteristics of the savanna and, as a result, facilitate the establishment of plant species which would ordinarily not be found in the open grassland and open savanna phases (Whittaker *et al* 1979). The micro-climate maintained by the bush cluster acts as a buffer against the effect of a variable physical environment providing a habitat with low resource stress due to high resource levels and supply rates of limiting soil resources and low rates of disturbance from fire (Grime 1979, Fuentes *et al* 1984, Tilman 1988, La Cock 1992). In such a habitat, interspecific competition can play a major role in determining the successional dynamics of the tree species found there. Although many tree species can co-exist in a stand if they differ in such factors as root distribution (Van Vegten 1983, Smith & Goodman 1987, Tolsma *et al* 1987) and life strategy traits (Teague 1989), species, which are ecologically equivalent for such characters, will replace one another over time as a function of their ability to utilize a limiting soil resource more efficiently at low levels or low rates of supply (Tilman 1988). Thus, it is evident that autogenic succession in

bush cluster structure will occur once the clump has been initiated (Smith & Goodman 1987, Archer 1988). Later, due either to drought conditions or some other factor affecting soil resource levels, cyclical succession (Yeaton 1978, 1988; Yeaton & Manzanares 1986; Valiente-Banuet & Ezcurra 1991) can maintain the species composition of the mature and coalesced bush clusters as well as that of the closed-canopy woodlands. In contrast, the open grassland and open savanna states experience higher resource stress due to lower soil resource levels and rates of supply and high rates of disturbance from fire (Grime 1979, Tilman 1988). Here, the ruderal features of early successional tree species should predominate as their successful establishment requires multiple and often long-distance dispersal events to open sites created by termites, ants and burrowing animals within the herbaceous layer.

In this study for example, early successional *Acacia* species, which initiate the bush clumps, are replaced by later successional *Acacia* species. Both groups of *Acacia* appear to be superficially, relatively more similar to one another than they are to the broad-leafed species which are also found in the later successional stages of the bush clusters. In actuality they are very different ecologically from one another (Hurt 1993). The early successional *Acacia* species have indehiscent pods which are eaten by several species of antelope. As a result, their seeds are dispersed widely over the landscape. The seeds of these early successional species appear to require open sites for germination and establishment within the herbaceous layer, such as those created by ants or termites or by animal scrapes (**personal obeservation**). Seedlings and saplings of early successional *Acacia* species are very shade sensitive (Smith and Goodman 1987, **personal observation**) and tend to grow as mono-layers (*sensu* Horn 1974). Later successional *Acacia* species have dehiscent pods which release their seeds while on the tree (Hurt 1993). Their wind-dispersed seeds have relatively short dispersal distances as a consequence. However, their seedlings and saplings are more shade tolerant than are those of the early successional *Acacia* guild and they are able to establish in the shade of the latter. In addition, they have a larger plant biomass due to their greater height and multi-layered growth habit and can overtop and shade out members of the early successional *Acacia* guild (Hurt & Yeaton 1992, 1993). Members of the later successional *Acacia* guild can also interact with broad-leafed later successional tree species in a cyclical succession. These *Acacia* species can establish

in small, and hence shady, light gaps caused by tree fall within the bush clump or closed-canopy forest and in turn, be shaded out over time by more shade tolerant broad-leafed species.

The strong positive relationship between cluster area and species richness suggests that many of the woody species that occur in the Natal bushveld are dependant on the clustered structure of the vegetation for establishment and survival (Chapter 2). This is a similar phenomenon to those observed in Texas (Whittaker *et al* 1979, Archer 1988), Chile (Fuentes *et al* 1984) and in the Eastern Cape Province, South Africa (La Cock 1992). Only a few species seem to be able to maintain large populations outside bush clusters. For example, although individual plants from 38 species were encountered outside woody vegetation clusters at `Darkest Africa', only four species comprised 80% of the individuals measured in the open grassland/open savanna state. On the same study site, individuals from 57 species were recorded in bush clusters, while eleven species made up 60% of the total population measured. Bush clusters are thus not only more species rich, but also more diverse.

Land use practices also have an important effect on the species richness of the bush clusters at the landscape level. In areas in which bush clusters have been reduced in number or in size through intense utilisation of wood resources, `bush clearing' operations, cultivation of crops, or by some natural phenomenon, species richness is greatly reduced. For example, mean cluster area declined from 82.1 $m^2$ at `Darkest Africa' , a site used only for light-to-moderate cattle grazing and low levels of wood cutting, to 62.1 m^2 at Weenen, a former labour farm now being rested and rehabilitated, to 12.4 m^2 at Mhlumba and 5.5 m^2 at Msinga, both of which sites had been labour farms in the past and continue still to be heavily overgrazed to this day. Concurrent with this change in mean bush cluster size, total species number recorded at each site declined from 57 species at `Darkest Africa' to 38 species at Weenen and 27 and 15 species at Mhlumba and Msinga respectively. The range of species encountered within a bush cluster also declined from two to 24 species at `Darkest Africa' to two to 16 at Weenen and two to 6 at both Mhlumba and Msinga. Such landscapes, where the bush cluster phase has been greatly reduced in size and number, are probably more `fragile' than landscapes with a well-developed bush cluster

phase. The `fragility' of these heavily disturbed landscapes arises in part from the reduced sizes of their bush clusters which make individual species' population sizes within a bush cluster low. Small bush clusters would be more susceptible to fire encroaching into their interiors. They would also suffer a loss in the buffering effect that a larger cluster would have on the climatic conditions within the bush cluster. As a result, small populations would periodically go extinct within the bush cluster and, because not only are the bush clusters smaller but also fewer in number on heavily disturbed landscapes, re-establishment of these species by immigration from other bush clusters and from closed-canopy woodlands would be greatly reduced (*e.g.* MacArthur and Wilson 1967). Thus, maintenance of the bush cluster phase in Natal bushveld is important for the maintenance of species diversity and, ultimately, for the maintenance of ecosystem resilience.

A two-phased pattern of bush cluster development is present in Natal bushveld. These phases are (i) an initial phase of cluster establishment with concentric expansion of the cluster perimeter, and (ii) a later phase where cluster growth is a function of coalescence between two or more bush clusters. This pattern of development is supported by the observation that larger clusters tend to become non-circular in shape. It is also supported by the fact that it was more difficult to identify over the 45-year period the same clusters from the three sets of aerial photographs used. Hence, the rate of cluster growth at the landscape scale will be a result of the density of individual trees, particularly *Acacia* spp., which might initiate the formation of new clusters under their canopies. In this case, the establishment of individuals of early successional species of *Acacia* and the absence of events that prevent cluster formation are the key factors influencing the development of Natal bushveld. Thus cycles of `bush encroachment' are necessary to maintain the bush cluster phase in this vegetation type.

Because of the strong observed relationship between species richness and bush cluster area, I have used species richness as an indicator of cluster development status rather than cluster area. Species richness is an explicit value that can easily be obtained by counting the number of species in a bush cluster while bush cluster area is difficult and time consuming to measure accurately. The use of cluster species richness also avoids the dilemma of possibly confusing large mono-specific thickets with well-developed woody vegetation clusters.

Indirect gradient analyses (ter Braak & Prentice 1988) by means of Detrended Correspondence Analysis (DCA)(Hill & Gauch 1980) for data on the proportional cover of different species in bush clusters indicates that the type and intensity of land use has the greatest impact on the composition of woody species in Natal bushveld landscapes (36% of the variation). As discussed above, bush clusters are smaller in size and fewer in number in situations where firewood gathering and grazing are most intense. When the study sites are compared to one another using DCA, the second axis represents a `succession' gradient that can be described by cluster species richness and explains 29% of the variation. When the land-use effect has been removed by analyzing data from the least disturbed site, `Darkest Africa', the first axis is the `successional' gradient (34% of the variation) and the second axis appears to be related to elevation and possibly topography (22% of the variation). These results show a similar trend to those of Archer *et al* (1988). However, unlike the results from the Texas study, DCA was unable to separate the clusters in this data set into discrete groups described by their species richness. There is however a clear continuum of increasing cluster species richness with a strong correlation between DCA axis scores and cluster species richness (Chapter 3). The `successional' gradient accounts for nearly a third of the variation observed in the distribution of species in the Natal bushveld which is remarkable as no attempt was made to minimize variation of other environmental variables such as slope angle, slope aspect and soil type which might affect plant species distributions.

These results support the assumptions that the distributions of plant species plants are not strictly governed by gradients in the physical environment (Van Hulst 1980) and that the effect of the physical environment is usually masked by biotic interactions among individual plants (Nott 1991). Furthermore, they accentuate the oversimplification that the framework of `primary' and `secondary' factors has in describing how savanna dynamics function (Teague & Smit 1992).

Cluster species richness can also be used to describe a continuum of successional developmental stages. For modelling purposes such stages could be classified as discrete Clementsian successional stages. Such use of Clementsian terminology helps to avoid the concept of convergence on a single `climatic climax' and can explain the development of varying successional pathways and endpoints in the

same landscape (MacMahon 1981). Plotting relative abundances of individual species along a gradient of increasing categories of species richness provides a model of successional species turnover for the bushveld in the Weenen District (Chapter 4). This model confirms successional pathways suggested for Natal bush veld and southern African bushveld generally (Bews 1917, Comins 1953, Killick 1959, Wells 1959, Edwards 1967, Morris 1967, Smith and Goodman 1987, Briers & La Cock 1991, Ben-Shahar 1991) and for rangelands in North America (Yeaton and Manzanares 1986, Archer *et al* 1988, Archer 1989, 1990 & Scanlan & Archer 1991) in which microphyllous, leguminous woody species are followed in succession by broad-leafed woody species and, in some instances, succulents. It also provides a more objective basis for the functional classification of woody plant species in the Natal bushveld into successional groups.

Functional classification of species groups was done on the basis of the proportional occurrence of individuals of a tree species in five categories of increasing species richness which have been assumed to represent different points along a successional gradient. Classification of a species to a particular functional group was done objectively by operationally defining its group on the basis of where it had reached 40% of its cumulative frequency distribution for its response curve. However, it must be kept in mind that the response curves for many of the species are based on small data sets ($n < 15$ individuals/species). Hence results should be used chiefly to generate hypotheses on the `successional status' of the different species and to illustrate the potential use of this method. More thorough description of individual species response to succession gradients fell outside the scope of this study.

Four types of response curves (and hence, four functional groups) were identified in this study. However, their functional status must be viewed as relative, not only to species in another group, but to the species within the group as well. Also, there may exist a hierarchy of `successional' status between and within groups. Functional Group 1 represents `pioneer' species which are either ruderal or generalists (Chapter 4). Members of this group are associated with small bush clusters or the vegetation outside bush clusters, and are probably indicative of a landscape that experiences a high degree of disturbance or is a open grassland undergoing a recent invasion of woody plant species. In contrast, Functional Group 4 represents `climax' species which are associated with well-developed bush clusters or closed-canopy woodland.

Species whose seeds are dispersed by large herbivores are limited to the `pioneer' end of the `successional status spectrum' while species with bird and wind dispersed seed are associated with the remaining stages of the `successional status spectrum'. Large herbivores readily utilise a variety of habitats and they can deposit large quantities of seed in their faeces in open areas away from woody cover (Gwynne 1969, Coe & Coe 1987, Brown & Archer 1987, Hurt 1993). Germination of these seeds and subsequent survival of seedlings may be enhanced by favorable micro-environmental conditions created by the dung (Brown & Archer 1987), escape from concentrations of seed predators (Coe & Coe 1987) and release from competition with established woody plants (Hurt & Yeaton 1992). In addition, the biomass of the herbaceous layer may be reduced by large herbivores, particularly in the vicinity of termite mounds (Smith & Yeaton, unpublished data), so that intensity of woody plant competition with grasses (Stuart-Hill & Tainton 1989, Skarpe 1990a) and the potential for the occurrence of `hot' fires is suppressed (Trollope 1982). It has also been suggested that soils under the open grassland state may be nitrogen deficient due to losses from frequent burning (Frost *et al* 1986). Hence, the ability of many *Acacia* species to fix nitrogen (Dye & Spear 1982; Furniss, unpublished data, & Granger & Yeaton, unpublished data) may give them a competitive advantage over other tree species during the initial stages of `bush encroachment'.

The ability of the early successional functional group to establish and survive outside bush clusters suggest that successful germination and survival of large numbers of these `pioneer' species are event driven. The occurrence of seemingly even-aged, mono-specific stands of these early successional tree species offer support to the concept of event-driven establishment (Comins 1953, Edwards 1967, Acocks 1988). Any combination of events that increase (i) the amount of viable seed that is produced, (ii) the dispersal of viable seed into grasslands, (iii) the germination of seed, or (iv) the survival of seedlings should lead to the establishment of these early successional trees in the open grassland state in such stands. Such events seem to operate at different temporal scales, and are often the result of a combination of circumstances. Examples of circumstances that can lead to such establishment events are:

i) The introduction or extinction of large herbivores on the rangeland (Janzen 1986, Fuentes *et al* 1986, Archer 1989, 1990).

ii) Periods of above average rainfall (Archer 1990).

iii) Intense utilisation of the herbaceous layer by herbivores (Skarpe 1990a,b).

iv) Reduction in the density of seed predators (Coe & Coe 1987).

v) Reduction in the intensity and frequency of fires (Trollope 1982, Frost 1985, Sabiiti & Wein 1988).

vi) Increased depth of the ground water table (Tinley 1982).

vii) Intense disturbance of the soil characteristics such as what happens with ploughing or sheet erosion (Joubert 1966, Van Vegten 1983, Tolsma *et al* 1987).

viii) Removal or reduction of browsers from the ecosystem (Owen-Smith 1989, Frost *et al* 1986, Teague 1989).

In contrast to the above, woody plant species in the later successional groups are either bird or wind dispersed. Birds are generally more habitat specific than are large herbivores and the seed shadows created by birds are relatively small. As a result, birds rarely disperse seeds of plant species that are restricted to bush clusters or to closed-canopy woodland into open grassland unless some form of perching structure is available to them (McDonnell & Stiles 1983, Fuentes *et al* 1984, Izhaki *et al* 1991). In arid and semi-arid regions, most bird-dispersed seeds will probably have germination or seedling survival difficulties even if they were dispersed into open sites (Fuentes *et al* 1984, 1986; Briers & La Cock 1991; La Cock 1990). In addition, the seed shadow for trees with wind-dispersed seeds is also relatively small and is related to the density of woody plant cover (Fuentes *et al* 1984, Eldridge *et al* 1991, Kigomo *et al* 1991). Thus, the rate of range expansion on the landscape by woody plants with bird- or wind-dispersed seeds is related to the rate of invasion of open areas by woody plants with large herbivore-dispersed seeds. The invasion of later successional functional species is therefore a slow process of diffusion (Fuentes *et al* 1986) and demonstrates that current ideas of bush clearing to optimise short-term range management objectives can have serious negative implications for the long-term objective of maintaining ecosystem resilience and productivity at the landscape scale.

Direct assessment of change in woody cover and individual cluster area over time from aerial photographs yielded results that were again dependent on the previous land use history of the site (Chapter 5). Woody plant cover on the light-to-moderately grazed and relatively undisturbed `Darkest Africa' site increased during the period 1940-

1985 after showing a slight decline suring the drought years of 1940-1964. In contrast, on the Weenen site, which had been severely overutilized in the past and is now being rested and rehabilitated, a dramatic decrease in woody plant cover occurred during the drought period of 1940-1964 (when the area was still being heavily utilized as a labour farm) which had only just begun to recover by 1985. The areas of bush clusters at the relatively undisturbed `Darkest Africa' site showed an increase during the 1940-1964 drought period, declining slightly in the wetter 1964-1985 period. The decline in bush cluster area could be due to a loss of trees at the margins of the bush cluster from `hot' wildfires resulting from the increased fuel load represented by the herbaceous layer during wet periods. The results obtained in this study are relatively the same as those obtained by Archer *et al* (1988) for southeastern Texas savannas. In each case prolonged drought events seem to kill individual woody plants while larger clusters remain intact. During periods of above average rainfall there seem to be increased establishment, survival and growth of woody plants outside bush clusters and subsequent cluster growth through the coalescence of smaller clusters.

`Bush encroachment' in KwaZulu-Natal seems to be a cyclical, event driven, phenomenon. When viewed at long-term time scales, pulses of `bush encroachment' and the subsequent break-up of the closed-canopy woodland and the clustered phases of savanna landscapes are responsible for the maintenance of woody species richness in the Natal bushveld. Savanna landscapes in KwaZulu-Natal can be classified into two broad categories;

(i) young bushveld, characterised by the dominance of the open grassland and open savanna phases or, alternatively, by mono-specific thickets of `pioneer' species. The bush cluster phase, when present, will be comprised of early successional or mid-successional functional species.

(ii) old bushveld, characterised by a well-developed, closed-canopy woodland and large, coalesced bush cluster. Alternatively, if there has been significant disturbance to the landscape, old bushveld may be characterised by many small remnant bush clusters comprised of large individuals of `late successional' species. In either case, the open savanna state will be dominated by individual early successional functional species and the proportion of the landscape represented by the open grassland state would be small.

As discussed previously, succession in young bushveld is initiated by

`germination survival events' and is then driven by facilitation. Successional processes in young bushveld may be arrested by recurrent disturbances such as fire (Trollope 1982, Frost 1985), drought (Archer 1990), frost (Smit 1990), and competition between seedlings of `pioneer' woody plants and grass (Knoop & Walker 1980, Stuart-hill & Tainton 1989) but are essentially autogenic in time (Archer *et al* 1988). In old bushveld, succession becomes cyclical and is driven by competition. Here, well-developed bush clusters provide a buffer against the effects of variable disturbance regimes such as fire, drought and frost. Both old and new bushveld may be superimposed on the same landscape due to intense utilization by humans in the recent past. The net result of such a superimposition is an often undecipherable mosaic of successional states and woody plant species composition.

Interpretation of the dynamics of this vegetation is further complicated by the relatively species rich and diverse vegetation component of landscapes in this region of KwaZulu-Natal. This high plant species diversity can be ascribed to the dynamic juxta-position of various southern African `biomes'. Furthermore, the rough physiognomy of the landscape offers a wide variety of habitats that can act as potential refuge sites and/or dispersal nodes (Werger 1979, Cowling *et al* 1989). Viewed at a long time scale, various cycles of invasion by different `biomes' is evident (Goodman 1991). These operate mainly along a north-south orientated gradient from the tropics towards more temperal areas along the east coast of southern Africa, and at the same time along an east-west orientated altitudinal gradient from the coast to the inland areas. These `biome' shifts can possibly be explained as shifts in the distribution patterns of `primary' determinants of vegetation distribution such as climatic changes (Emanuel *et al* 1985a,b; Ellery *et al* 1991). However, this may be an oversimplification as the long, intense utilisation of the interior basins of KwaZulu-Natal by farmers (Maggs 1980, 1989; Feeley 1978, 1987; Granger & Prins 1991) may have hastened these shifts. The most important effect that agriculture has had on the vegetation of KwaZulu-Natal during the last 2000 years is probably the degree to which the landscape has been transformed to the open grassland and open savanna states. Such transformation has facilitated the establishment of `pioneer' woody species and, in so doing, initiated an autogenic succession process which was accelerated by intense cattle grazing during the Late Iron Age, *c* 500 to 1000 years ago (Guy 1989, Maggs

1989). This transformation was further intensified with the arrival of European settlers during the nineteenth Century. These later settlers not only controlled the burning of these savannas to a greater degree than the previous land users but also exterminated many of the megaherbivores (*sensu* Owen-Smith 1988) from the region (Smithers 1986). Control of burning enhanced the successful establishment of early successional woody species in these rangelands, and the elimination of large animals, such as elephant and rhinocerus, which create and maintain the open grassland and savanna states (Buechner & Dawkins 1961, Laws 1970, Norton-Griffiths 1979, Dublin *et al* 1990), has led to further `bush encroachment'.

In any event, these cycles of biogeographic change are important to the maintenance of biodiversity in the KwaZulu-Natal landscape. Simplification and fragmentation of ecosystems by management to arrest change for the sake of short and medium-term production objectives and by conversion to monocultures at the landscape scale are probably the most serious threats to the long-term maintenance of species richness, resilience and productivity of landscapes in KwaZulu-Natal.

CHAPTER SEVEN : CONCLUSIONS

This study of the structure and functional dynamics of the Natal bushveld has yielded many results in common with those of Archer and his co-workers (*op. cit.*) for a relatively similar situation in the savannas of southeastern Texas. However, there are some differences which can be attributed to the topological complexity of the Natal bushveld sites and to the wider range of land use histories which they have experienced. Below, I state what I believe the major conclusions are of this work are and wherever possible point out the similarities and differences with the savannas of North America.

First, cluster species richness can be used as a index of cluster developmental stage. This is particularly important where a variety of different land use histories must be considered. Heavily used rangelands often have fewer bush clusters per unit area and they are smaller, whereas relatively unutilised areas have a higher density of bush clusters and a greater range of bush cluster sizes. As a result of the differential effects of immigration to and extinction within bush clumps, cluster species richness is a better estimate of successional stages in areas with different land use histories. This effect was not a problem at the La Copita site in the savanna of southeastern Texas which was subjected to only one pattern of land use history.

Second, cluster growth is dependant on the rate at which different clusters can coalesce, and not concentric expansion of individual cluster perimeter. This, in turn, is dependent on the rate of cluster formation and survival. A similar result was obtained in Texas. In both studies, cluster formation and survival were greatest during wet periods with severe mortality of small bush clusters occurring during periods of longterm drought. Larger bush clusters continued to increase in size in both studies during drought periods and were difficult to identify individually in the sequence of aerial photographs used. The latter observation suggests that the estimates of the rate of closure of the bush cluster phase are lower than they actually are.

Third, most of the species that occur in the Natal bushveld seem to be dependent on the clustered structure of woody vegetation for establishment and survival. Very few of the species found in the interstices of the bush cluster phase are present within the bush clusters. Those species that are present in both situations are primarily members of the genus, *Acacia*, or are understory shrubs which rarely reach tree size. A similar result was reached in the Texas study where *Prosopis glandulosa*

is the dominant woody species found in the open grassland stage. It also serves as foci for the establishment of other woody species, which are rarely found in the open, under their canopies. As a consequence, the cluster phase in Natal bushveld vegetation is important for the maintenance of species diversity and ecosystem resilience at the landscape scale. The bush cluster phase is particularly important where different types of land use are employed on the landscape. The effects of these land-use practices can (i) result in local extinction of species and loss of ecosystem resilience and (ii) retard the development of closed-canopy woodland.

Fourth, a `successional gradient', which is likely the result of biotic interaction among individual plants over a `successional time scale' can be used to explain the pattern of species distribution in a Natal bushveld community to a large degree. As a consequence, species responses to such an `successional gradient' can be used to describe the temporal range of individual species, and to group these species into functional classes. In this study, as in the La Copita study, the early successional species are aggressive invaders of the grassland phase and are not easily removed once established. These species are primarily responsible for our `bush encroachment' problems in southern Africa and in many other parts of the world. In all cases, the propagules of these early successional species are dispersed into grasslands by large vertebrates. The propagules of later successional species are dispersed by birds, monkeys and, rarely, wind. These species are generally broad-leafed and appear to be dependent on bush clusters to facilitate their successful establishment.

Next, models based upon the above methods and results can be constructed which describe species turn-over in bushveld communities along a continuum of `successional' development. Such a model can be used to classify different communities or sites on the basis of their species composition according to their previous land-use history and their successional status. Such a model would be a potentially useful management and planning tool.

Finally, the phenomenon of `bush encroachment' in southern Africa is the result of natural events in which man has interceeded. Unless a clear understanding is obtained of the dynamics underlying the ecological processes and the environmental forces involved in causing the transition from one state of vegetation to another within these rangelands, no attempts to manage this vegetation to a desired endpoint will be successful in the long term. At present, bush clusters in Natal bushveld continue to grow and coalesce in moderately disturbed veld, slowly reverting to closed-canopy woodland. The future of Natal bushveld under higher levels of disturbance is still an

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APPENDIX

Table 1. DCA scores of first two axes, species richness and study site for 113 clusters from DA, WE and MHL.

Site	Species Richness	Axis 1	Axis 2	Site	Species Richness	Axis 1	Axis 2
DA	6	170	284	WE	3	47	174
DA	2	233	275	WE	10	61	171
DA	4	150	244	WE	2	37	170
DA	9	140	214	WE	12	38	169
EB	3	177	238	WE	5	87	167
EB	5	177	238	we	7	105	165
WE	4	105	235	EB	4	162	164
EB	5	188	229	DA	3	138	158
DA	5	118	224	DA	12	165	153
EB	4	280	218	EB	5	212	152
KE	4	145	210	DA	10	192	150
DA	3	103	202	WE	10	29	148
WE	3	103	202	WE	4	50	145
DA	6	137	196	EB	6	193	144
WE	2	175	179	KE	3	274	142
EB	2	175	179	DA	6	84	142
KE	2	175	179	KE	4	274	142
EB	2	175	179	WE	2	101	141
WE	3	175	179	WE	2	101	141
EB	2	175	179	KE	5	101	141
EB	3	175	179	WE	2	101	141
EB	4	175	179	WE	7	31	139
EB	4	175	179	WE	6	125	138

Continued ...

KE	3	175	179
EB	2	175	179
EB	3	175	179
DA	6	84	177
EB	4	244	176
WE	5	83	119
WE	8	56	119
DA	11	121	118
WE	14	22	113
WE	8	76	113
DA	5	184	113
WE	4	70	111
WE	4	75	110
WE	5	155	110
DA	12	183	106
WE	3	109	105
WE	7	26	105
WE	5	89	104
EB	4	226	101
EB	3	226	101
EB	3	226	101
EB	2	226	101
EB	3	226	101
EB	4	226	101
WE	3	57	100
WE	6	24	100
DA	4	136	96
WE	12	0	90
WE	11	41	132
WE	7	67	129
WE	9	34	123
KE	6	189	122
WE	5	105	121
WE	3	78	76
WE	4	67	73
DA	21	99	72
WE	11	37	70
WE	6	87	70
EB	5	219	69
WE	6	52	67
EB	6	275	63
WE	6	59	63
KE	3	225	62
KE	5	225	62
DA	5	240	60
WE	7	75	60
DA	9	172	57
DA	13	197	56
DA	15	178	54
DA	15	97	54
DA	12	139	53
DA	12	134	49
DA	9	191	43
DA	11	73	28
DA	18	98	26
DA	22	148	25

Continued ...

EB	7	225	86	EB	6	176	16
DA	9	91	86	DA	11	181	0
WE	4	65	83	DA	5	171	78
KE	6	213	83	DA	14	112	78
EB	6	240	81	WE	7	34	77
WE	16	1	80				

Table 2. DCA scores of 1st two axes and cluster species richness for 32 clusters from the DA study site.

Cluster	Species Richness	Axis 1	Axis 2	Cluster	Species Richness	Axis 1	Axis 2
1	6	261	50	17	4	87	107
2	2	248	0	18	5	79	89
3	4	231	91	19	14	70	155
4	9	228	72	20	13	69	41
5	5	215	60	21	5	69	25
6	3	196	149	22	9	62	58
7	6	195	40	23	21	61	154
8	6	164	157	24	15	58	67
9	12	152	56	25	9	49	85
10	10	145	18	26	12	46	48
11	3	145	109	27	15	34	89
12	6	143	194	28	22	33	97
13	11	128	142	29	12	29	17
14	5	115	85	30	218	12	125
15	12	111	16	31	1221	2	82
16	9	91	128	32	11	0	25